SHOUT
SHARE
IT

HARVARD UNIVERSITY

Ernst Mayr Library
of the Museum of
Comparative Zoology

124

MCZ
LIBRARY
SEP 29 1992
HARVARD
UNIVERSITY

THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. 55, No. 1, pp. 1–56 August 30, 1992

A Genus Level Revision of Western Hemisphere Lygaeinae (Heteroptera: Lygaeidae) with Keys to Species[1]

ALEX SLATER[2]

TABLE OF CONTENTS

Abstract 2
Introduction 2
Materials and Methods 3
Acknowledgements 3
Placement of *Davidedoviellaxis* Brailovsky 3
Key to Western Hemisphere Genera and Subgenera of Lygaeinae 3
Genera and Subgenera 5
Achlyosomus new genus 5
Acroleucus Stål 6
Anochrostomus new genus 9
Biblochrimnus Brailovsky 10
Craspeduchus Stål 10
Dalmochrimnus Brailovsky 12
Ektyphonotus new genus 13
Hadrosomus new genus 14
Latochrimnus Brailovsky 15
Lygaeospilus Barber 16
Lygaeus Fabricius 17
Melacoryphus A. Slater 19
Melanopleurus Stål 21
Neacoryphus Scudder 23
Nicuesa Distant 23
Ochrimnus Stål 24
Ochrimnus (*Aglaochrimnus*) new subgenus 27
Ochrimnus (*Ochrimnus*) Stål 28
Ochrimnus (*Orthochrimnus*) new subgenus 29
Ochrimnus (*Parochrimnus*) new subgenus 30
Ochrimnus (*Phaeochrimnus*) new subgenus 30
Ochrostomus Stål 31
Oncopeltus Stål 32
Oncopeltus (*Erythrischius*) Stål 34
Oncopeltus (*Oncopeltus*) Stål 35
Orsillacis Barber 35
Oxygranulobaphus Brailovsky 36
Pseudacroleucoides Brailovsky 37
Torvochrimnus Brailovsky 38
Phylogenetic Analysis 39
Methodology 39
Characters Not Used in the Analysis 40
Character Analysis 43
Relationships 48
Literature Cited 53
Addendum 56

[1]CONTRIBUTION NUMBER 3086 FROM THE DEPARTMENT OF ENTOMOLOGY, UNIVERSITY OF KANSAS, LAWRENCE, KANSAS 66045.

[2]JAMES A. SLATER II. PRESENT ADDRESS: 523 ELM STREET, LAWRENCE, KANSAS 66044. ALEX SLATER IS USED TO AVOID CONFUSION IN THE LITERATURE WITH THE AUTHOR'S FATHER, J. A. SLATER.

ABSTRACT

The lygaeid subfamily Lygaeinae is revised at genus level for the western hemisphere. A total of 22 genera and seven subgenera are recognized. Four genera and four subgenera are newly described. One genus is removed from synonymy. Four genera are placed in synonymy (one with a genus in another subfamily). The generic placement of many species is changed. A key to western hemisphere genera is provided, as are keys to western hemisphere species for genera containing more than one species. Each genus and subgenus is described or redescribed. A list of species and a brief synopsis of their distributions are included for each genus and subgenus. Line drawings of the head, metapleuron, spermatheca, ovipositor, clasper, and aedeagus are provided for each genus and subgenus, based on the type species when possible. A cladistic analysis of those lygaeine genera restricted to the western hemisphere is provided. The genera *Lygaeus* and *Oncopeltus* were excluded from the analysis on the hypothesis that their presence in the western hemisphere is the result of relatively recent dispersal from the eastern hemisphere. The analysis resulted in 30 equally parsimonious trees. A phylogeny based on these 30 trees is proposed.

INTRODUCTION

The subfamily Lygaeinae is unusual among Lygaeidae in containing many large, brilliantly colored species. As a result many species have been described. More than one-sixth of all species covered in Slater's (1964a) catalogue of the Lygaeidae belong to the subfamily Lygaeinae.

The current generic classification of the subfamily is based primarily on the works of Stål (1868, 1872, 1874). He introduced many new characters, including the shape of the posterior pronotal margin, presence or absence of a longitudinal median pronotal carina, surface sculpture of the scutellum, shape of the costal margin of the corium, shape of the posterior metapleural margin, and the extent of development of the ostiolar peritreme. In addition to these structural characters he used the color of the ostiolar peritreme and the presence or absence of a pale spot on the vertex of the head. He defined most eastern hemisphere genera and subgenera using structural characters but most western hemipshere genera and subgenera on the basis of color and the lack of structural features defining other genera. As pointed out by Slater (1964b) and by Ashlock (1975), this reliance on color, while useful in that it allows species to be assigned to genera, tends to obscure phylogenetic relationships among species.

Since the works of Stål no comprehensive treatment of the subfamily for either eastern or western hemisphere has been attempted, although many genera and species have been described from both hemispheres. The vast majority of these new genera were erected to contain single, distinctive, newly discovered species.

Recent work on eastern hemisphere genera (Scudder, 1963; Seidenstücker, 1964; Štys, 1972; A. Slater, 1985) has emphasized the importance of structural characters, especially of the male and female external genitalia. Unfortunately, with the exception of Scudder (1965), Ashlock (1975), and A. Slater (1988), such characters have rarely been used for western hemisphere genera. In this paper I have relied heavily on the male and female genitalia in assigning species to genera. The result is the reassignment of many species to existing genera as well as the erection of several new genera and subgenera.

The cladistic analysis is based on the almost certainly paraphyletic group of genera restricted to the western hemisphere. Though accepting the general premise that cladistic analyses should be done on holophyletic groups, I believe that analysis of paraphyletic groups may also be of value. In fact, many analyses of non-vertebrates are carried out on paraphyletic groups, if for no other reason than our imperfect knowledge of the fauna at the species level. The chief problem with cladistic analysis of paraphyletic groups is the loss of information on characters and their states resulting from exclusion of some taxa. This is of special importance when the distributions of character states among taxa are incongruent. In that case there is a clear danger that the most parsimonious resolution will differ if more taxa are added to the analysis. Thus the phylogeny resulting from analysis of a paraphyletic group must be considered a tentative hypothesis.

In the case of the western hemisphere Lygaeinae there is some evidence (e.g., the presence of highly developed lobes, often bearing spines, on the conjunctiva and/or vesica) that the majority of genera do comprise a holophyletic group. Of the genera excluded from that group one *(Orsillacis)* appears to represent a very early branching of the lygaeine lineage, two (*Acroleucus* and *Nicuesa*) form a very well defined group also probably branching early, and the rest (*Ektyphonotus, Pseudacroleucoides,* and *Torvochrimnus*) are of uncertain placement. When selecting characters and determining their polarity, I examined a subset of the eastern hemisphere lygaeine fauna. I am therefore reasonably certain that the characters, and their states, used in the analysis reflect conditions in the subfamily as a whole. Thus, while this analysis must be considered provisional, I believe it provides not only a sound base of characters upon which further work may be built but also a reasonable estimate of the evolutionary history of the subfamily in the western hemisphere.

MATERIALS AND METHODS

Specimens representing about 85% of the described western hemisphere species were examined. Generic placement of those species not seen was based on published descriptions.

Distributions are based on both published records and examined specimens. Because distributions are given only at the genus level, they are not affected by the difficulty of assigning older literature records to presently recognized species.

Measurements of overall length were taken both from the literature and from examined specimens using an ocular micrometer in a binocular dissecting microscope. Specimens to be measured were selected by eye as representing the smallest and largest available specimens for a genus. Listed measurements are rounded to the nearest half millimeter.

Male and female genitalia were prepared using methods described by A. Slater (1985) except that the entire abdomen was removed from the specimen and soaked in the surfactant before removal of the genitalia. This was done so that the tergum could be examined for the presence of laterotergites and so that the intersegmental muscles of the sternum could be examined. The tergum and sternum were carefully separated and internal organs were removed to expose the intersegmental sternal musculature. This method of exposing the musculature was not always successful.

Drawings were made with the aid of a camera lucida attached to a binocular dissecting microscope. Magnifications of 27X, 54X and 72X were used. A scale line is included with each figure, the equivalence of that line in millimeters for each subfigure being indicated in the figure legend. All genitalia drawings were made with the structure to be drawn supported by cotton wool immersed in water in an excavated glass block. Claspers were oriented so that the opening at the base of the shank was perpendicular to the microscope's plane of focus. Aedeagi were oriented so that the left side of the phallotheca was parallel to the microscope's plane of focus. Ventral views of ovipositor valves were obtained by tearing the membrane connecting the valvifers and then inserting the valvifers in cotton wool. This allowed the valvulae to be held apart so that the medial connecting membrane could be examined.

Prior to the work of Ashlock (1957, 1967), and in most work following those two papers, descriptions and figures of the lygaeid phallus were based on material pulled out of the phallotheca but not inflated. This method produces a distorted view of the relative lengths and shapes of the conjunctiva and vesica. Only the most obvious features such as sclerites and very large lobes are recognizable, and the shape and true proportions of the lobes are often not accurately portrayed. For this reason I have relied on Ashlock's (1957) illustrations and descriptions as the basis for my interpretation of the lygaeine phallus.

Keys to species are based in part on published keys and descriptions and in part on examination of specimens. Because I have not seen all species included, and because the keys are not based on species-level revisions of genera and so may not take into account the full extent of intraspecific variability, they must be considered provisional. Many of these keys bear little resemblance to those on which they are based. Any errors should be attributed to me rather than to the author of an original key.

Publications containing keys upon which I have drawn heavily are: for *Acroleucus*, Brailovsky, 1980; for *Biblochrimnus*, Brailovsky, 1982c; for *Dalmochrimnus*, Brailovsky, 1984b,d; for *Hadrosomus* and *Torvochrimnus*, Brailovsky, 1983b; for *Lygaeus*, Brailovsky, 1978b; for *Latochrimnus*, Brailovsky, 1984c; and for *Ochrimnus*, Brailovsky, 1982a. The key to *Lygaeospilus* is that of Scudder, 1981. The key to *Melacoryphus* is that of A. Slater, 1988.

Cladistic analysis was carried out using the microcomputer version (2.4) of the PAUP maximum parsimony computer program (Swofford, 1985). The analysis was carried out with the following parameters set: SWAP=GLOBAL; MULPARS; ROOT=ANCESTOR; HOLD=15; MAXTREE=100; OPT=FARRIS. The program was also run with OPT=DELTRAN and OPT=MINF set to determine alternative placements of individual characters on the resulting trees.

ACKNOWLEDGEMENTS

I would like to thank the following individuals for the loan of specimens upon which this work is based: Richard C. Froeschner, National Museum of Natural History; Randall T. Schuh, American Museum of Natural History; Peter D. Ashlock, Snow Entomological Museum, The University of Kansas; Paul H. Arnaud, Jr., California Academy of Sciences; Saul Frommer, University of California, Riverside; Robert O. Schuster, University of California, Davis; Harry Brailovsky, Instituto de Biologia, Universidad Nacional Autónoma de México; David A. Rider, Louisiana State University; James A. Slater, University of Connecticut. Loans of eastern hemisphere material were listed in A. Slater (1985).

I thank the following individuals for reading and commenting on the manuscript: James S. Ashe, George W. Byers, Leonard C. Ferrington, Jr., and Charles D. Michener, all of the University of Kansas. I am especially appreciative of Dr. Ashe for his willingness to take on the major burden of critical review on short notice and with little time available for completion of the task.

Craig C. Freeman, Kansas Biological Survey, University of Kansas, kindly provided access to the PAUP computer program.

Special thanks go to Virginia H. Ashlock and Geraldine G. Slater, who provided invaluable help in preparation of the manuscript.

Last, but far from least, I would like to take this opportunity to express my deep appreciation of Peter D. Ashlock. He not only supervised most of the research resulting in this paper, but also profoundly influenced the development of my philosophic approach to systematics. I deeply regret that he was not able to see the completed work and can only hope that it would have met with his approval.

PLACEMENT OF *DAVIDEDOVIELLAXIS* BRAILOVSKY

Brailovsky (1982b) erected the genus *Davidsonia* to contain the single newly described species *arnaudi*. As *Davidsonia* was preoccupied he later (1983a) proposed *Davidedoviellaxis* as a replacement name. Examination of the type (and only known) specimen shows it to belong to the genus *Eremocoris* of the subfamily Rhyparochrominae. I therefore place *Davidedoviellaxis* Brailovsky (= *Davidsonia* Brailovsky (preocc.)) as a junior synonym of *Eremocoris* Fieber (Rhyparochrominae, Drymini).

KEY TO WESTERN HEMISPHERE GENERA AND SUBGENERA OF LYGAEINAE

1. Scutellum distinctly punctate; antennal segment I not reaching apex of tylus ..... *Orsillacis*
—Scutellum impunctate; antennal segment I surpassing apex of tylus 2
2. Eyes carried on stalks; sternum VII of female not cleft medially but rather produced posteriorly ..... *Nicuesa*
—Eyes at most slightly produced; sternum VII of female cleft medially 3
3. Hemelytral membrane dark brown to black with apical margin or rounded macula at extreme apex hyaline; raised callus of anterior pronotal lobe interrupted just mesad of shiny callar impressions, separated from distinct median carina by depressed area ..... *Acroleucus*

—Hemelytral membrane opaque, if appearing hyaline (greasy) then white with contrasting darker veins; raised callus of anterior pronotal lobe uninterrupted 4
4. Series of 4 transverse impressions behind callus of anterior pronotal lobe ..... *Ochrimnus* . 5
—No series of transverse impressions behind callus of anterior pronotal lobe, at most a shallow interrupted punctate depression 9
5. Abdominal sterna III-VI either red (sometimes with yellow posterior margins on some segments) or black with yellow posterior margins ..... *Ochrimnus (Aglaochrimnus)*
—Abdominal sterna III-VI if with red markings then either predominantly yellow with transverse red marks or variegated with red, yellow, and brown, never black with yellow posterior margins 6
6. Abdominal sternum VI of female about 1/3 as long medially as laterally; anterior pronotal lobe either completely orange or yellow or with margins pale yellow and disc orange, red, or brownish red, or if anterior lobe with extensive dark markings then entire pronotum brown except narrow pale margins and narrow pale longitudinal median line not significantly broader posteriorly ..... *Ochrimnus (Phaeochrimnus)*
—Abdominal sternum VI of female about equally long medially and laterally; anterior pronotal lobe with extensive dark markings, usually connected with dark markings of posterior lobe, dark markings of posterior lobe either separated by a pale longitudinal median line distinctly broader posteriorly than anteriorly or without median line, or if anterior lobe without dark markings then posterior lobe also without dark markings 7
7. Pronotum subquadrate, predominantly dark brown with pale markings yellow; base of corium and clavus pale; apical margin of corium completely pale and much broadest at apical angle ..... *Ochrimnus (Orthochrimnus)*
—Pronotum much narrower anteriorly than posteriorly, often predominantly orange; base of corium and clavus dark; apical margin of corium if completely pale then about equally broad throughout 8
8. Robust; posterior lobe of pronotum usually predominantly orange or predominantly dark brown with orange lateral and posterior margins, if with extensive dark maculae on either side of midline then basal 2/3 of corium dark brown and apical 1/3 orange; disc of anterior pronotal lobe brown without pale median line ..... *Ochrimnus (Ochrimnus)*
—Slender; posterior lobe of pronotum pale yellow or orange with extensive dark macula on either side of midline or if without dark markings than anterior lobe also without dark markings; corium never brown basally and orange apically; anterior lobe often with pale median longitudinal line ..... *Ochrimnus (Parochrimnus)*
9. Scutellum swollen, median carina indistinct; pronotum produced posteriorly at each side of scutellum ..... *Oncopeltus* . 10
—Scutellum not swollen, median carina distinct; pronotum not produced posteriorly at each side of scutellum 11
10. Hemelytral membrane dark brown to black except sometimes with small white maculae; hairs of lateral pronotal margin longer, thicker and more upright than those on hemelytra ..... *Oncopeltus (Oncopeltus)*
—Basal angle of hemelytral membrane pale, concolorous with adjacent part of corium; hairs of lateral pronotal margin similar to those of hemelytra ..... *Oncopeltus (Erythrischius)*
11. Posterior pronotal lobe at most as high mesally as at lateral margin, disc flat or nearly so, median carina distinct in at least basal third 12
—Posterior pronotal lobe higher mesally than at lateral margin, disc distinctly convex, median carina obsolete 15
12. Clavus pale with contrasting dark veins ..... *Neacoryphus*
—Clavus unicolored 13
13. Pubescence of dorsum very dense, short, upright ..... *Dalmochrimnus*
—Pubescence of dorsum sparse, short, decumbent, sometimes interspersed with long upright hairs 14
14. Length more than 6mm; hemelytral membrane of macropter usually black, sometimes with white corial margin or white with contrasting dark veins ..... *Melacoryphus*
—Length less than 6mm; hemelytral membrane of macropter usually mottled with white or with large white spot ..... *Lygaeospilus*
15. Pronotum coarsely punctate, punctations extending onto disc of posterior lobe ..... *Oxygranulobaphus*
—Pronotum finely punctate, punctations restricted to depressed areas just before and behind callus of anterior lobe 16
16. Pronotum dark except humeral angles sometimes red ..... *Melanopleurus*
—Pronotum with extensive pale areas or at least with more than humeral angles pale 17
17. Veins of clavus either lighter or darker than surrounding areas 18
—Veins of clavus concolorous with surrounding areas 19
18. Lateral margins of posterior pronotal lobe brown; corial veins darker than surrounding areas ..... *Torvochrimnus*
—Lateral margins of posterior pronotal lobe pale; corial veins lighter than surrounding areas ..... *Hadrosomus*
19. Scutellar margin of clavus pale, contrasting with dark corial margin or semicircular submedian macula 20
—Clavus unicolored or pale basally and dark apically or with only commissural margin pale 21
20. Apical margin of corium with yellow border 22
—Apical margin of corium orange with narrow black border ..... *Anochrostomus*
21. Postcallar impression interrupted at each side of midline; pronotum with disc of anterior lobe pale, or dark except narrow margins and narrow median longitudinal pale line reaching anterior margin ..... *Craspeduchus*
—Postcallar impression not interrupted at each side of midline; pronotum with disc of anterior lobe dark except broad margins, pale median line, if present, not approaching anterior margin ..... *Ochrostomus*
22. Pronotum slightly longer medially than wide anteriorly; hemelytral membrane brown with pale longitudinal median stripe ..... *Ektyphonotus*
—Pronotum distinctly shorter medially than wide anteriorly; hemelytral membrane dark brown to black, white, or pale with contrasting dark veins, never with pale median stripe 23

23. Costal margin of corium pale basally and apically, dark brown to black between; dark markings of corium either restricted to costal margin and a small discal spot or a triangular macula with longest side at costal margin; thoracic pleura almost entirely gray or black ..... *Lygaeus*
—Costal margin of corium usually entirely pale, if interrupted then dark markings of corium forming a subrectangular spot with anterior and posterior edges straight; thoracic pleura with wide pale margins at least posteriorly and on acetabulae 24
24. Length more than 10mm; posterior pronotal lobe with at most small dark macula near posterior margin ..... *Biblochrimnus*
—Length less than 7mm; posterior pronotal lobe with at least a large brown macula at each side of midline and covering most of disc 25
25. Head swollen dorsally, strongly declivent; ocelli distinctly lower than vertex when viewed laterally; length less than 4.5mm ..... *Pseudacroleucoides*
—Head not swollen dorsally, moderately declivent; ocelli about level with vertex when viewed laterally; length at least 4.7mm 26
26. Pale margins of pronotum and corium very narrow, indistinct; disc of anterior pronotal lobe dark brown except a very narrow median longitudinal line ..... *Achlyosomus*
—Pale margins of pronotum and corium broad, distinct; if disc of anterior pronotal lobe dark brown except very narrow median longitudinal line then costal margin of corium interrupted medially by subrectangular black macula ..... *Latochrimnus*

GENERA AND SUBGENERA

Achlyosomus new genus
(Fig. 1)

Type species: *Neacoryphus beutelspacheri* Brailovsky, 1979c.

Included species: *Achlyosomus beutelspacheri* (Brailovsky), 1979c (*Neacoryphus*); *A. campestris* (Brailovsky), 1979c (*Neacoryphus*).

BODY. Moderately robust; impunctate except immediately before and behind callus, on prosternum, and on propleuron anteriorly and posteriorly; hairs short, dense, decumbent. Length 5.0-6.5mm. *Head* (fig. 1a) moderately declivent; vertex convex; ocellus distinctly raised above surface mesally, directed laterad, distance between ocelli about seven times distance from ocellus to eye; buccula slightly to moderately produced, ventral margin moderately convex. *Pronotum* with posterior width about twice anterior width; medial length slightly less than anterior width; anterior margin concave, raised, beaded laterally, separated from callus by depressed area with shallow, profuse punctation, most strongly depressed laterally; posterior margin slightly convex; lateral margins convex anteriorly and posteriorly, slightly concave behind callus; callus distinct laterally, indistinct mesally, callar impressions unbranched, extreme apex and mesal third almost transverse, otherwise curving evenly toward anterior angles; impression behind callus shallow, with shallow punctation, interrupted medially by low carina. *Scutellum* with length about 0.7 times width; stem and arms of median carina broad; lateral fovea distinct posteriorly, bottom smooth anteriorly, transversely striate posteriorly. *Hemelytron* just surpassing apex of abdomen; corial veins distinct, slightly raised; membrane opaque. *Propleuron* divided into three parts by dorsoventral impressions, anterior and posterior parts with shallow punctation, median part impunctate and almost flat. *Mesopleuron* divided into anterior and posterior sections by dorsoventral impression, impunctate. *Metapleuron* (fig. 1c) impunctate; posterior margin directed dorsoventrally, almost straight, posterior margin of acetabula produced slightly posteriorly; ostiolar peritreme (fig. 1b) with anterior margin of channel much higher than posterior margin and with apical button short, rounded, and distinctly separated from surrounding pleuron dorsally and posteriorly; evaporative area small, subquadrate, surrounding dorsal part of peritreme, reaching margin of mesopleuron. *Abdomen* without anterolateral scars; sternum II fully exposed; sternum VI of female about three-fourths as long medially as laterally; sternum VII of female cleft to base. *GENITALIA*. — *Clasper* (fig. 1e) with blade at a slightly oblique angle to shank, at most as long as shank, curved, flattened, twisted so that inner face is somewhat ventrally directed; posterior projection short but distinct, broad; shank without rooflike interior projection, a well defined posterior ridge extending onto base of blade dorsally, separated from a more anterior ridge by a distinct groove, anterior ridge variable in length, with a subtriangular projection somewhere along its length. *Aedeagus* (fig. 1g) bending before telescoping into phallotheca; conjunctiva very short, attached to phallotheca basad of phallothecal apex, without subapical projections; ejaculatory reservoir connected basally to surrounding membrane by winglike sclerites; vesica with ventral, laterally directed basal lobes arising from winglike sclerites, distad of basal lobes fairly symmetrically swollen, without projections though constricted to form three or four indistinct lobes; ring sclerite obsolete; gonoporal process (fig. 1f) long, robust; secondary gonopore with extremely elongate, robust process almost closed dorsally; phallotheca with entire dorsal margin flanged, process short, flared laterally. *Spermatheca* (fig. 1d) with basal tube thick, of moderate length, without distinct swollen area; apical tube at most lightly pigmented basally, becoming more heavily pigmented apically, broad basally, rapidly becoming much thinner than basal tube; apical bulb elongate, complexly coiled, not distinctly separated from adjoining tube. *Ovipositor* moderately elongate; first valve (fig. 1h) with connecting membrane extending beyond apex of valvula about half valvular length, median cleft reaching about half distance to base, distinct secondary cleft laterad of median cleft forming secondary projection to about level of valvular apex, without strongly pigmented or sclerotized areas; second valve (figs. 1i,j) with connecting membrane cleft almost to base, valvula almost flat except for elongate bulge along dorsal margin, apical third slightly

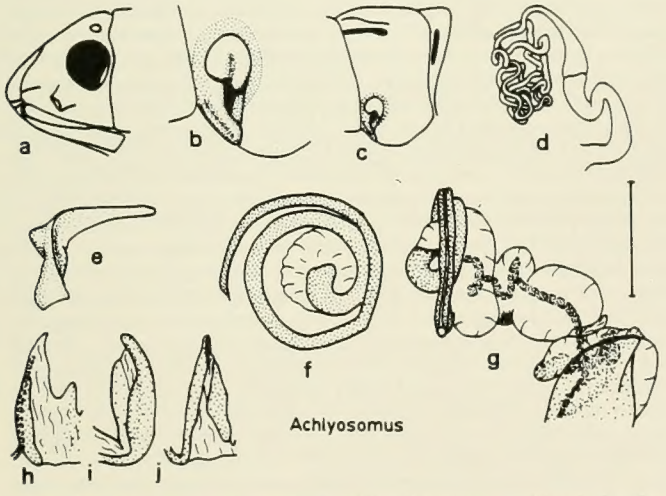


Fig. 1. *Achlyosomus beutelspacheri* (Brailovsky). a. Head. b. Ostiolar peritreme and evaporative area. c. Metapleuron. d. Spermatheca. e. Left clasper, right lateral view. f. Gonoporal process. g. Partially inflated aedeagus, left lateral view. h-j. Ovipositor, left valvula and connecting membrane: h, first valve, ventral view; i, second valve, lateral view; j, second valve, ventral view. Scale (mm): a,c = 1.0; b,d,h-j = 0.5; e-g = 0.375.

convex. *COLOR.* — *Head* either dark brown to black or yellowish except bucculae pale yellow. *Pronotum* brown, darkest at humeri, posterior lobe with thin light brown or yellow longitudinal median macula. *Scutellum* brown, stem of median carina light brown or yellow. *Hemelytron* brown, palest at basal angle, darkest near apex of corium, claval suture and apical margin of corium narrowly light brown or yellow; membrane dark brown, without white apical margin. *Thoracic pleura* brown except anterior margin of pronotum, posterior margins, and acetabulae pale yellow. *Abdomen* ventrally with lateral margins pale brown, segments II-IV dark brown medially, segments V-VII sometimes with dark brown sublateral longitudinal macula.

DISTRIBUTION. Both species are known from only a few closely grouped localities in northeastern Colombia near the Venezuelan border.

COMMENTS. The name *Achlyosomus* is from the Greek and refers to the dark, indistinct markings of the body.

The two known species are very similar in both structure and color. They may be reliably separated only by the structure of the clasper. *Achlyosomus* species are most similar to some *Ochrimnus* and *Latochrimnus* species in external appearance. They may be separated from the former by the lack of a series of transverse slits behind the callus and from the latter by their generally darker coloration and more distinct punctation on the posterior pronotal lobe. The lateral lobes at the ventral juncture of vesica and conjunctiva, and their associated winglike sclerites, are unique among Lygaeinae.

KEY TO SPECIES OF *ACHLYOSOMUS*

1. Rostrum reaching posterior margin of metacoxa; ostiolar peritreme yellow; head dorsally with ocher lateral markings ..... *campestris*
—Rostrum reaching posterior margin of abdominal sternum II; ostiolar peritreme dark brown; head dorsally without pale lateral markings ..... *beutelspacheri*

Acroleucus Stål
(Fig. 2)

Acroleucus Stål, 1874: 99, 114. Type species: *Lygaeus coxalis* Stål, 1858, designated by Slater, 1964a.

Included species: *Acroleucus argutus* Brailovsky, 1980; *A. bordoni* Brailovsky, 1984a; *A. brevicollis* (Stål), 1862 (*Lygaeus*); *A. bromelicola* Brailovsky, 1977c; *A. caicaraensis* Brailovsky, 1984a; *A. conchatus* Brailovsky, 1984a; *A. coxalis* (Stål), 1858 (*Lygaeus*) = *Pamera flavicosta* Berg, 1879, fide Berg, 1883; *A. daedalus* Brailovsky, 1980; *A. delineatus* Distant, 1893; *A. devius* Brailovsky, 1980; *A. diaphanus* Brailovsky, 1984a; *A. dollingi* Brailovsky, 1980; *A. flavoseptus* Stål, 1874; *A. goellnerae* Brailovsky, 1980; *A. haemopterus* Stål, 1874; *A. herbosus* Brailovsky, 1984a; *A. heros* Breddin, 1904; *A. hoberlandti* Brailovsky, 1980; *A. inimicus* Brailovsky, 1980; *A. lamothei* Brailovsky, 1980; *A. marinoi* Brailovsky, 1980; *A. municeps* Brailovsky & Barrera, 1984; *A. neomaurus* Slater, 1964a = *Lygaeus maurus* Stål, 1858, preocc. fide Slater, 1964a; *A. nexus* Brailovsky & Barrera, 1984; *A. nigellus* Distant, 1893; *A. nigrovittatus* Stål, 1874; *A. nobilis* Stål, 1874; *A. orinocoensis* Brailovsky, 1984a; *A. phoenix* Brailovsky, 1980; *A. pothus* Breddin, 1904; *A. rubefactus* Distant, 1893; *A. scitulus* Brailovsky & Barrera, 1984; *A. signaticollis* Stål, 1874 = *Lygaeus calderensis* Distant, 1893, fide Brailovsky, 1982a = *Lygaeus sulcatus* Osborn, 1904, fide Brailovsky, 1980; *A. signoretii* Stål, 1874 = *A. sceleratus* Distant, 1893, fide Brailovsky, 1980; *A. stali* Slater, 1964a = *Lygaeus pallipes* Stål, 1858, preocc. fide Slater, 1964a; *A. subniger* Distant, 1882; *A. tullus* (Stål), 1862 (*Lygaeus*); *A. vittaticeps* Stål, 1874; *A. vulturnus* Brailovsky, 1984a; *A. yacambuensis* Brailovsky, 1984a.

BODY. Moderately robust, somewhat depressed, distinctly parallel sided; impunctate except on thoracic pleura; hairs short, fine, semi-upright, slightly longer, finer and sparser on thoracic pleura. Length 5.0-14.0mm. *Head* (fig. 2a) moderately declivent; vertex flat; ocellus distinctly raised above surface mesally and posteriorly, distance between ocelli about 3.5 times distance from ocellus to eye; eyes distinctly separate from anterior pronotal angles, thus appearing protuberant; buccula slightly or moderately produced, ventral margin either moderately convex or flat. *Pronotum* with posterior width two to four times anterior width; medial length about equal to anterior width; anterior margin concave, not raised, separated from callus by depressed impunctate area to each side of distinct median carina; posterior margin slightly convex; lateral margins straight anteriorly and either broadly rounded or almost straight posteriorly; callus distinct, interrupted medially by median carina and flanking depressions connecting ante- and postcallar depressed areas, callar impressions unbranched, slightly sinuate, mesally almost transverse, laterally curving evenly toward anterior pronotal angles; depressed area behind callus impunctate, interrupted by median carina and low lateral carina. *Scutellum* with length about 0.9 times width; arms of median carina slightly thicker than stem, forming shallow Y instead of T; lateral fovea distinct, bottom rugose. *Hemelytron* greatly surpassing apex of abdomen; corial veins distinct, slightly raised, more so basally; membrane opaque except apex hyaline. *Propleuron* divided into three parts by broad dorsoventral impressions; anterior and central parts narrow, convex, impunctate; posterior part broad, flat, indistinctly punctate. *Mesopleuron* impunctate; divided into two parts by dorsoventral impression; anterior part broad, flat; posterior part narrow, slightly convex. *Metapleuron* (fig. 2c) impunctate; posterior margin directed slightly anterodorsally, slightly convex; posterior margin of acetabula about as long as rest of posterior margin of pleuron, not produced posteriorly; ostiolar peritreme (fig. 2b) strongly produced, evaporative area large, subtriangular, extending onto posterior margin of mesopleuron. *Abdomen* without anterolateral scars; sternum II fully exposed; sternum VI of female about as long medially as laterally; sternum VII of female cleft to base. *GENITALIA.* — *Clasper* (fig. 2e) with blade usually at slightly oblique angle to shank, occasionally at about right angle to shank, from slightly shorter to slightly longer than shank, seldom more than slightly curved, moderately flattened, twisted so that inner face is somewhat ventrally directed; posterior projection distinct, thickness variable, conical or thumblike, sometimes bent apically so that apex is directed inward; shank with inner face often swollen at juncture with blade, this swelling separated by a shallow groove from a thick shelflike flange on inner face, flange often most produced at anterior or posterior end, sometimes extending onto base

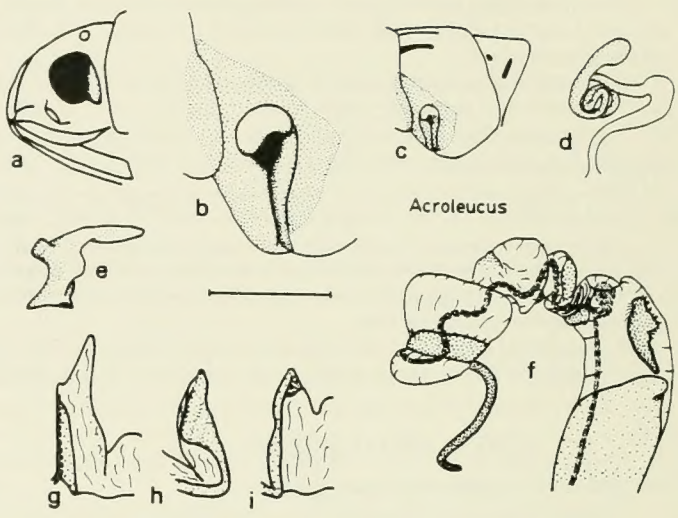


Fig. 2. *Acroleucus coxalis* (Stål). a. Head. b. Ostiolar peritreme and evaporative area. c. Metapleuron. d. Spermatheca. e. Left clasper, right lateral view. f. Partially inflated aedeagus, left lateral view. g-i. Ovipositor, left valvula and connecting membrane: g, first valve, ventral view; h, second valve, lateral view; i, second valve, ventral view. Scale (mm): a,c = 1.0; b,d,g-i = 0.5; e,f = 0.375.

of blade, line of attachment varying from subparallel with posterior margin of shank to subparallel with blade. *Aedeagus* (fig. 2f) telescoping directly into phallotheca; conjunctiva short, with large, heavily sclerotized, crescent-shaped subapical lateral lobes, without subapical dorsal lobe; vesica fairly symmetrically swollen throughout, without projections and slightly flattened basally, sometimes with a blunt projection medially; ring sclerite absent; helicoid process strongly developed apically, obsolete or represented by disconnected remnants basally; gonoporal process short; apical process of secondary gonopore short, narrow, acute; phallotheca with apical margin flanged dorsally, this flange extending onto short phallothecal process. *Spermatheca* (fig. 2d) with basal tube moderately long, slightly curved, swollen apically to varying degree, this swelling sometimes partly pigmented and with longitudinal axis same as that of tube; apical tube pigmented, inserted at about right angle to apical swelling of basal tube, about equal in thickness to basal tube, longer than basal tube, coiled; apical bulb usually about as long as basal tube, variable in shape but usually elongate and slightly enlarged apically. *Ovipositor* short, broad; first valve (fig. 2g) with connecting membrane extending at least one-third length of valvula beyond apex of valvula, cleft medially to at least half distance to base, often with a low rounded projection at base of cleft, a lightly pigmented ridge between valvula and cleft but without sclerites, valvifer either slender and subtriangular or with basal half expanded toward center of membrane with a notch at mesal angle of base; second valve (figs. 2h,i) with membrane cleft to at most half distance to base, a low rounded projection at base of cleft sometimes reaching level of apex of valvula, sometimes an ovate longitudinal pigmented or sclerotized area on each side of midline; valvula very narrow basally, becoming broad and flat apically, usually broadest subapically, apex often highly sculptured, sometimes with spines or flanges. *COLOR.* — Extremely variable, ranging from almost completely black or brown to almost completely red, orange, or yellow. *Head* varying from completely dark to completely pale; bucculae usually pale yellow. *Pronotum* varying from completely dark to completely pale, often pale with either transverse or longitudinal dark maculae. *Scutellum* varying from completely dark except pale apex to completely pale. *Hemelytron* varying from completely dark to completely pale, at least base of costal margin usually pale; membrane usually dark brown to black with either broad apical margin or small apical spot with digitiform extension toward disc clear. *Thoracic pleura* usually pale with central infuscation. *Abdomen* ventrally varying from completely dark to completely pale.

DISTRIBUTION. Mexico to Argentina. Distributional information for *Acroleucus* species is very limited. Of the 40 described species, fully three-fourths are known from either a single locality or from only two nearby localities. All but 11 species are endemic to South America.

COMMENTS. The interruption of the callus of the anterior pronotal lobe by longitudinal depressions flanking a distinct median carina is diagnostic for the genus. The elongate, inwardly bent aeromicropyles of the egg are unique among Lygaeidae (although given the apparent close relationship of species of *Acroleucus* with *Nicuesa* species, the unknown eggs of the latter may be similar). The bucculae of the type species, *A. coxalis,* are more produced and have a more sinuate ventral margin than do the bucculae of most other *Acroleucus* species.

Despite much variation in size and color, members of *Acroleucus* form a remarkably homogenous group. There is considerable interspecific variation in the development of the basal swelling of the spermatheca and of the medial flattened part of the first valvifer. Many species are known from only one or a few specimens of a single sex. Because there is some indication of sexual dimorphism in the genus, it is quite possible that some of the described species represent different sexes of the same species and will be combined when better series are available.

KEY TO SPECIES OF *ACROLEUCUS* STÅL

1. Trochanters dark brown or black 2
—Trochanters yellow or ocher 10
2. Coxae black 3
—Coxae orange or yellow 7
3. Head dorsally entirely black 4
—Head dorsally orange except black apex of tylus 5
4. Clavus and corium entirely black ..... *vulturnus*
—Base of clavus and corium to about apex of scutellum yellow ..... *nobilis*
5. Pronotum without distinct black spots, anterior and posterior margins infuscated; scutellum without one or more black basal spots ..... *inimicus*
—Pronotum with distinct black spot over callus to either side of midline; scutellum with black median basal spot 6
6. Humeral angles orange; rostrum reaching base of abdominal sternite VII ..... *pothus*
—Humeral angles black; rostrum reaching base of abdominal sternite IV ..... *bordoni*
7. Abdominal sterna black ..... *heros*
—Abdominal sterna orange 8
8. Posterior pronotal margin broadly black ..... *subniger*
—Pronotum entirely orange 9
9. Hemelytra orange with scattered yellow markings ..... *goellnerae*
—Hemelytra black except extreme base ..... *phoenix*
10. Translucent apex of hemelytral membrane with digitiform extension toward center of membrane 11
—Translucent apex of hemelytral membrane not extended toward center of membrane 12
11. Head dorsally, except apex of tylus, yellow; rostrum not reaching anterior margin of prosternum ..... *bromelicola*
—Head dorsally black with diffuse pale markings; rostrum reaching anterior margin of prosternum ..... *coxalis*
12. Hemelytral membrane, except translucent apex, ocher or variegated with yellow and brown markings and veins yellow 13
—Hemelytral membrane, except translucent apex, dark brown to black 17
13. Head dorsally reddish without conspicuous black markings; hemelytral membrane with irregular series of small dark brown spots near apex ..... *delineatus*

—Head dorsally red or yellow with distinct black median line; hemelytral membrane completely ocher or with single dark basal spot or variegated brown and yellow with yellow veins 14
14. Antennal segment IV yellow with black apex; hemelytral membrane variegated brown and yellow with veins yellow; clavus and corium yellow with area around claval suture infuscated ..... *lamothei*
—Antennal segment IV black; hemelytral membrane ocher with at most a single brown basal spot; clavus and corium orange and black 15
15. Pronotum and corium orange with black markings a continuation of median dorsal line of head ..... *marinoi*
—Pronotum and corium completely yellow or black with narrow orange lateral margins 16
16. Pronotum, clavus, and corium yellow ..... *orinocoensis*
—Pronotum black with orange lateral margins; clavus and corium black except basal spot on clavus and costal margin of corium orange ..... *dollingi*
17. Head dorsally black, if light markings present then restricted to vertex or area between ocellus and eye 18
—Head dorsally orange or yellow, often with black longitudinal median line of varying width 28
18. Lateral margins of pronotum dark brown to black 19
—Lateral margins of pronotum at least partly yellow or orange 22
19. Anterior margin of pronotum ocher ..... *neomaurus*
—Anterior margin of pronotum dark brown to black 20
20. Corium entirely black ..... *conchatus*
—Corium predominantly reddish orange or ocher 21
21. Clavus and corium entirely reddish orange ..... *haemopterus*
—Clavus and corium ocher with broad longitudinal black line posterior to scutellum ..... *municeps*
22. Posterior margin of pronotum distinctly completely yellow or orange 23
—Posterior margin of pronotum usually at least partly dark brown or black, if completely yellow or orange then margin very narrow and visible only in posterior view 25
23. Anterior pronotal margin black medially ..... *diaphanus*
—Anterior pronotal margin yellow or orange 24
24. Costal margin of corium yellow, becoming broader apically, apical margin broadly yellow ..... *flavoseptus*
—Costal margin of corium orange, becoming narrower apically, apical margin black or very narrowly orange ..... *brevicollis*
25. Pronotum with broad median longitudinal yellow line ..... *devius*
—Pronotum dark brown to black medially or with very narrow median pale line 26
26. Corium predominantly pale orange-yellow ..... *scitulus*
—Corium predominantly dark brown or black with narrow yellow or orange costal margin 27
27. Yellow lateral pronotal margin narrow, usually not including humeral angles ..... *tullus*
—Yellow lateral pronotal margins broad, almost meeting immediately posterior of callus, including humeral angles ..... *caicaraensis*
28. Femur and tibia predominantly yellow or pale brown 29
—Femur and tibia predominantly dark brown to black 30
29. Veins of hemelytral membrane black, contrasting with dark brown surrounding areas ..... *signaticollis*
—Veins of hemelytral membrane dark brown, concolorous with surrounding areas ..... *stali*
30. Pronotum entirely black 31
—Pronotum at least partly orange, yellow, or red 32
31. Corium black except narrow costal margin ocher ..... *vittaticeps*
—Corium yellow except apical angle black ..... *argutus*
32. Pronotum entirely orange 33
—Pronotum at least partly dark brown or black 34
33. Corium completely orange ..... *rubefactus*
—Apical third of corium black ..... *daedalus*
34. Midline of pronotum completely dark brown to black 35
—Midline of pronotum at least partly yellow, orange, or red 37
35. Corium black except narrow ocher costal margin; pronotum black except dark orange posterior half of lateral margin ..... *nexus*
—Corium either completely black or completely yellow or orange except sometimes black claval and apical margins; pronotum yellow or orange with broad median longitudinal black area 36
36. Longitudinal median black pronotal area with margins subparallel; antenniferous tubercles at least partly black ..... *nigrovittatus*
—Longitudinal median black pronotal area subtriangular, broadest posteriorly; antenniferous tubercles orange ..... *nigellus*
37. Pronotum predominantly red or orange, dark markings restricted to posterior margin and a macula at mesal end of each callar impression 38
—Pronotum predominantly dark brown to black, light markings restricted to margins and midline 39
38. Anterior pronotal maculae C-shaped; scutellum completely black ..... *yacambuensis*
—Anterior pronotal maculae round; scutellum predominantly orange ..... *signoretii*
39. Pronotal midline and margins, except humeral angle, yellow; corium completely black ..... *herbosus*
—Pronotal midline and margins red; corium black with small basal red mark ..... *hoberlandti*

Anochrostomus new genus
(Fig. 3)

Type species: *Lygaeus formosus* Blanchard, 1840.

Included species: *Anochrostomus formosus* (Blanchard), 1840 (*Lygaeus*) - *Lygaeus elatus* Stål, 1862, fide Stål, 1874.

BODY. Robust; impunctate except pronotum immediately before and behind callus and on prosternum and pro- and mesopleura; hairs short, fine, decumbent, moderately dense except sparse on hemelytron and posterior lobe of pronotum. Length 10.0-11.5mm. *Head* (fig. 3a) moderately declivent; vertex slightly convex; ocellus distinctly raised above surface mesally and posteriorly, distance between ocelli about eight times distance from ocellus to eye; buccula slightly to moderately produced, ventral margin slightly convex. *Pronotum* with posterior width slightly less than 1.7 times anterior width; medial length slightly greater than anterior width; anterior margin concave, slightly raised but not beaded laterally, separated from callus by indistinctly punctate area; posterior margin convex; lateral margins almost straight, slightly convex anteriorly and posteriorly, an indistinct constriction just behind callus; callus indistinct, callar impressions with short posterior branch about one-third distance from mesal end, transverse medially, curving anterad laterally; shallow impression behind callus extending well onto posterior lobe to give lateral margin a swollen appearance, coarsely punctate just behind callus, interrupted medially by distinct carina, not interrupted laterally. *Scutellum* with length about 0.8 times width; stem and arms of median carina about equally broad; lateral fovea shallow, most distinct anteriorly, bottom smooth, occasionally with a few shallow, transverse impressions. *Hemelytron* surpassing apex of abdomen; corial veins distinct, slightly raised. *Propleuron* divided into three parts by very shallow dorsoventral impressions, anterior part and posterior impression distinctly, finely punctate, median part slightly convex. *Mesopleuron* divided into anterior and posterior sections by very shallow dorsoventral impression, posterior part indistinctly punctate. *Metapleuron* (fig. 3c) impunctate; posterior margin directed dorsoventrally, convex, posterior margin of acetabula not produced posteriorly; ostiolar peritreme (fig. 3b) with anterior margin of channel much higher than posterior margin, apical button rounded, distinctly separated from surrounding pleuron dorsally and posteriorly; evaporative area small, surrounding dorsal part of peritreme. *Abdomen* without anterolateral scars; sternum II fully exposed; sternum VI of female about two-thirds as long medially as laterally; sternum VII of female cleft to base. *GENITALIA.* — *Clasper* (fig. 3e) with blade at right angle to shank, constricted basally, slightly longer than shank, moderately curved, somewhat dorsoventrally flattened, twisted so that inner face is somewhat ventrally directed; posterior projection very well developed, thick, subconical; shank without rooflike interior projection, a posterior longitudinal ridge on inner face with short acute projection at about middle separated from anterior hooked projection at juncture with blade by a shallow groove, a deep groove anterior and basad of hooked projection. *Aedeagus* (fig. 3i) bent before telescoping into phallotheca; conjunctiva short with large, bifid, subapical, lateral lobes, each apex armed with a single stout spine; vesica short, very broad basally, without projections proximad or distad of ring sclerite; ring sclerite incomplete, without projections; gonoporal process (fig. 3j) short, robust; secondary gonopore with extremely elongate acute process almost closed dorsally to form a secondary channel (fig. 3j); phallotheca without flange along apical margin, process short, extending toward phallothecal disc basally, flared laterally. *Spermatheca* (fig. 3d) with basal tube short, thick, without swelling; apical tube very long, thin, unpigmented except for irregularly coiled, heavily pigmented section just basad of apical bulb; apical bulb narrow, elongate, acute apically, sharply bent at base. *Ovipositor* moderately elongate; first valve (fig. 3f) with connecting membrane extending beyond apex of valvula about two-thirds valvular length, cleft to about half distance from base, lightly pigmented area between cleft and valvula but not connected with either, Y-sclerite distinct, extending around apex of membrane laterad of cleft; second valve (figs. 3g,h) with connecting membrane cleft medially about half distance to base, with distinct shoulder at each side of cleft, valvula strongly swollen subapically. *COLOR.* — *Head* black except bucculae and distinct, round macula at vertex ocher; antennae and rostrum dark brown to black. *Pronotum* with anterior lobe black; posterior lobe red-orange except small rounded black macula on either side connected with black anterior lobe, and large transversely ovate macula on either side just in front of posterior margin dark brown to black, and yellow area between anterior and posterior maculae and on posterior margin area behind about lateral two-thirds of posterior macula. *Scutellum* black. *Hemelytron* with clavus dark brown to black along corial margin, yellow along scutellar margin and claval suture; corium red-orange except large subtriangular discal macula and very narrow apical margin dark brown to black; membrane opaque white except variable basal margin dark brown. *Thoracic pleura* dark brown to black except anterior margin of propleuron and acetabular and posterior margins of all pleura narrowly ocher; an ovate area near posterolateral angle of each pleuron darker than rest of pleuron. *Abdomen* dark mottled brown, posterior margins of sterna IV-VI often light brown.

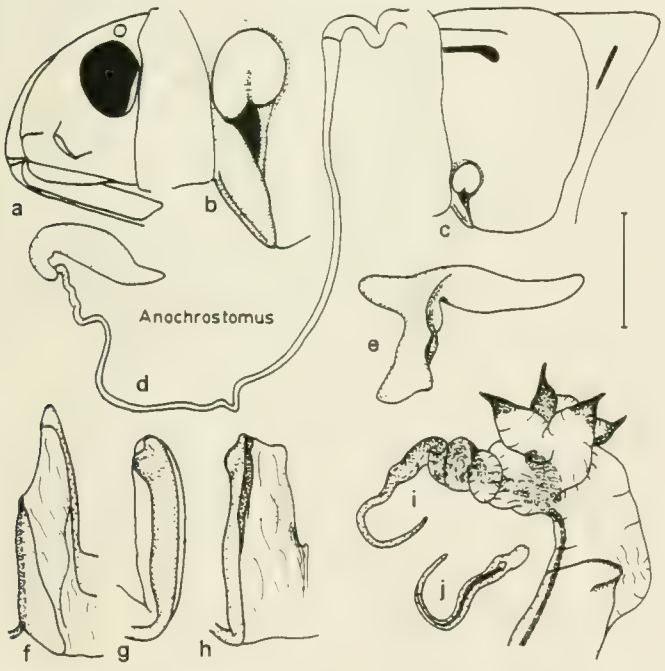


Fig. 3. *Anochrostomus formosus* (Blanchard). a. Head. b. Ostiolar peritreme and evaporative area. c. Metapleuron. d. Spermatheca. e. Left clasper, right lateral view. f-h. Ovipositor, left valvula and connecting membrane: f, first valve, ventral view; g, second valve, lateral view; h, second valve, ventral view. i. Partially inflated aedeagus, left lateral view. j. Gonoporal process. Scale (mm): a,c = 1.0; b,d,f-j = 0.5; e = 0.375.

DISTRIBUTION. The single species has been reported from southern Baja California, extreme southern Texas, and extreme southern Florida, south to Panama. There are records from many Caribbean islands and a single suspect record from Venezuela.

COMMENTS. The name combines the Greek prefix *an-* (not) with the generic name *Ochrostomus* and is intended to indicate close relationship between the two genera.

The single species of *Anochrostomus* is easily recognized by its coloration. In external appearance it is similar to *Lygaeus* species, with which it was formerly placed, except that the apex of the ostiolar peritreme is not elongate and is more distinctly separated from the surrounding metapleuron. The spine-bearing subapical lobes

of the conjunctiva, reduction of the distal part of the vesica, and spermatheca are very similar to those of *Ochrostomus* species, but the process of the secondary gonopore and the clasper are dissimilar. The dorsal pubescence of *Anochrostomus*, moderately dense on the anterior pronotal lobe and very sparse on the posterior lobe, is the best external character separating it from *Ochrostomus*.

Biblochrimnus Brailovsky
(Fig. 4)

Biblochrimnus Brailovsky, 1982a: 136. Type species: *Lygaeus* (*Ochrostomus*) *subcarinatus* Stål, 1874, original designation.

Included species: *Biblochrimnus carinicollis* (Bergroth), 1893 (*Lygaeus* (*Ochrostomus*)); *Biblochrimnus lindskogi* (Brailovsky), 1982c; *Biblochrimnus subcarinatus* (Stål), 1874 (*Lygaeus* (*Ochrostomus*)).

BODY. Robust; impunctate except for a few coarse punctures on pronotum before and behind callus and on thoracic pleura; hairs moderately sparse on head and disc of pronotum, moderately dense on hemelytron, densest on abdominal venter, short, fine, semidecumbent, interspersed with a few longer upright hairs medially on abdominal venter. Length 11.2-12.5mm. *Head* (fig. 4a) moderately declivent, vertex moderately convex; ocellus slightly raised above surface mesally and posteriorly, distance between ocelli about five times distance from ocellus to eye; buccula moderately produced, ventral margin moderately convex. *Pronotum* strongly declivent from back to front; posterior width about twice anterior width; medial length slightly greater than anterior width; anterior margin raised, most distinctly laterally, not beaded, separated from callus by shallow, punctate depression; posterior margin slightly convex laterally, slightly concave medially; lateral margins almost straight anteriorly, tumid and slightly convex posteriorly; callus low, distinct, callar impressions branched, slightly curved, sinuate; postcallar impression shallow, indistinctly punctate, not reaching lateral margin, interrupted medially by indistinct carina; disc of posterior lobe convex, slightly higher than lateral margins, flattening laterally. *Scutellum* with length about 0.8 times width; stem and arms of median carina broad, stem becoming lower apically; lateral fovea becoming indistinct apically, bottom smooth. *Hemelytron* considerably surpassing apex of abdomen; corial veins distinct, distinctly raised; membrane opaque. *Propleuron* divided into three parts by shallow dorsoventral impressions; impressions with shallow, fine punctation. *Mesopleuron* divided into two parts by indistinct dorsoventral impression; with shallow, fine punctation posteriorly. *Metapleuron* (fig. 4c) impunctate; posterior margin directed slightly posteroventrally, almost straight, posterior margin of acetabula not produced posteriorly; ostiolar peritreme (fig. 4b) with anterior margin of channel higher than posterior margin, apical button rounded, distinct from surrounding pleuron dorsally and posteriorly; evaporative area small, surrounding dorsal part of peritreme, reaching anterior margin of pleuron anteriorly. *Abdomen* without anterolateral scars; sternum II fully exposed; sternum VI of female about two-thirds as long medially as laterally; sternum VII of female cleft to base. *GENITALIA.* — *Clasper* (from descriptions and figures of Brailovsky, 1982c) with blade at oblique angle to shank, broad dorsoventrally, flattened, curved inward, twisted so that inner face is somewhat ventrally oriented; shank somewhat shorter than blade, posterior projection distinct, thumblike. *Aedeagus* unknown but probably with spine-bearing lobes at apex of conjunctiva. *Spermatheca* (fig. 4g) with basal tube short, thin, without swelling; apical tube elongate, thin, coiled and pigmented apically; apical bulb distinct, elongate, narrow, apex acute, base sharply bent. *Ovipositor* short; ring sclerites very thick, triangular; first valve (fig. 4d) with connecting membrane extending beyond apex of valvula by about one-third length of valvula, cleft medially almost to base, a secondary cleft laterad of median cleft resulting in short lateral and longer medial projection, Y-sclerite absent, a suboval sclerite between central cleft and valvula; second valve (figs. 4e,f) with connecting membrane replaced almost entirely by a thick sclerite, cleft to about one-fifth distance to base, valvula flattened except slightly convex subapically. *COLOR.* — *Head* yellow or orange with tylus and area around eye dark brown to black. *Pronotum* yellow to orange with a dark brown to black macula laterally on callus and laterally on posterior lobe near posterior margin. *Scutellum* dark brown laterally, pale medially, at least at apex. *Hemelytron* brown except costal margin, apical margin and claval commissure yellow or orange; membrane brown except for narrow white apical margin. *Thoracic pleura* orange or yellow, sometimes with dark maculae. *Abdomen* ventrally yellow, sometimes with infuscate areas.

DISTRIBUTION. Each of the three species is known from only a few localities, one from Colombia and Peru, one from Bolivia, and one from southeastern Brazil.

COMMENTS. Members of *Biblochrimnus* are very similar in general appearance to members of *Hadrosomus* but are much more robust. The extreme sclerotization of the second valve of the ovipositor is unique within the Lygaeinae. Though I have not seen the aedeagus, the presence of very well-developed pockets in the membrane at the base of the ovipositor indicates that either vesical or, more probably, apical conjunctival spines are present.

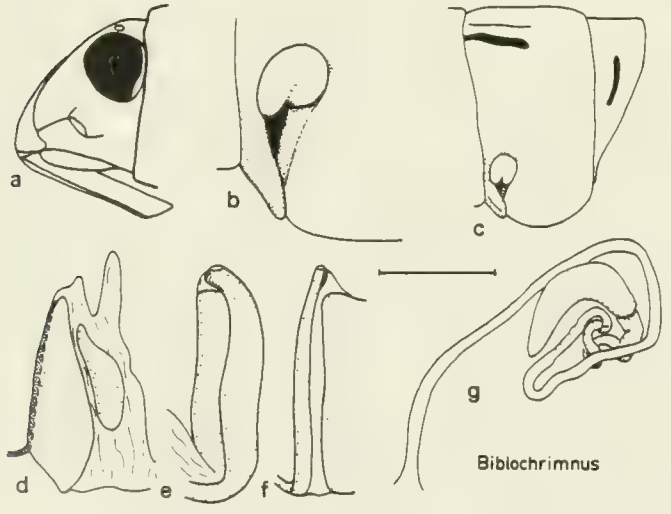


Fig. 4. *Biblochrimnus subcarinatus* (Stål). a. Head. b. Ostiolar peritreme and evaporative area. c. Metapleuron. d-f. Ovipositor, left valvula and connecting membrane: d, first valve, ventral view; e, second valve, lateral view; f, second valve, ventral view. g. Spermatheca. Scale (mm): a,c = 1.0; b,d-g = 0.5.

KEY TO SPECIES OF *BIBLOCHRIMNUS* BRAILOVSKY

1. Metasternal scent gland yellow ..... *subcarinatus*
—Metasternal scent gland black 2
2. Prosternum with a round black mark posteriorly; femora black ..... *lindskogi*
—Prosternum without a black mark; femora orange-brown ..... *carinicollis*

Craspeduchus Stål
(Fig. 5)

Lygaeus (*Craspeduchus*) Stål, 1874: 105, 109. Type species: *Lygaeus xanthostaurus* Herrich-Schäffer, 1847, designated by Van Duzee, 1916. *Craspeduchus* Slater, 1964a: 47.

Included species: *Craspeduchus buenoi* (Brailovsky), 1979c (*Neacoryphus*), **n. comb.**; *Craspeduchus circumseptus* (Stål), 1867 (*Lygaeus*), **n. comb.**; *Craspeduchus matudai* Brailovsky, 1979b; *Craspeduchus nigrolimbatus* Stål, 1874 (*Lygaeus* (*Craspeduchus*)); *Craspeduchus variegatus* (DeGeer), 1773 (*Cimex*),

n. comb. = *Cimex erythrochlorus* Gmelin, 1790, fide Stål, 1874 = *Lygaeus pulcher* Fabricius, 1803, fide Dallas, 1852; *Craspeduchus xanthostaurus* (Herrich-Schäffer), 1847 (*Lygaeus*) = *Lygaeus maurus* Walker, 1872, fide Distant, 1901.

Incertae sedis species: *Craspeduchus attrahens* Brailovsky & Barrera, 1984.

BODY. Robust; impunctate except immediately before and behind callus and on prosternum and propleuron; hairs short, moderately dense, decumbent. Length 7.0-9.5mm. *Head* (fig. 5a) moderately declivent; vertex convex; ocellus slightly raised above surface, distance between ocelli about five times distance from ocellus to eye; buccula moderately produced, ventral margin moderately convex. *Pronotum* with posterior width about two times anterior width; medial length about equal to anterior width; anterior margin concave, beaded, separated from callus by punctate depression; posterior margin subsinuate, slightly concave medially, slightly convex laterally; lateral margins straight; callus slightly swollen, callar impressions branched mesally, curving evenly toward anterior angles; impression just posterior to callus with sparse, shallow punctation, interrupted medially by low carina and laterally by raised area. *Scutellum* with length about 0.7 times width; stem and arms of median carina broad; lateral fovea distinct, bottom smooth. *Hemelytron* slightly surpassing apex of abdomen; corial veins distinct, slightly raised; membrane opaque. *Propleuron* divided roughly into thirds by punctate dorsoventral impressions, medial third slightly convex. *Mesopleuron* divided roughly into halves by impunctate dorsoventral impression. *Metapleuron* (fig. 5c) impunctate; posterior margin angled slightly anterodorsad, concave, posterior margin of acetabula produced slightly posteriorly; ostiolar peritreme (fig. 5b) with anterior margin of channel higher than posterior margin, apical button distinct from surrounding pleuron dorsally and posteriorly; evaporative area small, a semicircle surrounding dorsal part of peritreme. *Abdomen* without anterolateral scars; sternum II fully exposed; sternum VI of female about half as long medially as laterally; sternum VII of female cleft to base. *GENITALIA.* — *Clasper* (fig. 5e) with blade at oblique angle to shank, long, curved, flattened, twisted so that inner face is somewhat ventrally directed, posterior projection thumblike, elongate, thin, shank without rooflike interior projection, curved longitudinal ridge on inner face extending onto base of blade, inner face anterior of ridge concave with short longitudinal ridge near base and short oblique ridge near juncture with blade. *Aedeagus* (fig. 5i) bent before telescoping into phallotheca; conjunctiva with hooked, spine-bearing lateral lobe on each side near apex; vesica with large, conical ventral lobe at base, with distinct membranous hook distad of ring sclerite; ring sclerite reduced, lightly sclerotized; gonoporal process elongate, slender, coiled; process of secondary gonopore short, slender, acute; phallotheca without apical flange, process a short C-shaped flange broadest dorsally. *Spermatheca* (fig. 5d) with basal tube long, slender, without swelling; apical tube extremely elongate, slender and complexly coiled; apical bulb not differentiated from adjacent tube. *Ovipositor* short; first valve (fig. 5f) with connecting membrane extending about half length of valvula beyond apex of valvula, cleft medially about to two-thirds distance to base, lightly pigmented area between Y-sclerite and valvula, Y-sclerite strongly sclerotized, stem short and broad, arms reaching about level with apex of valvula, valvifer triangular, valvula triangular with

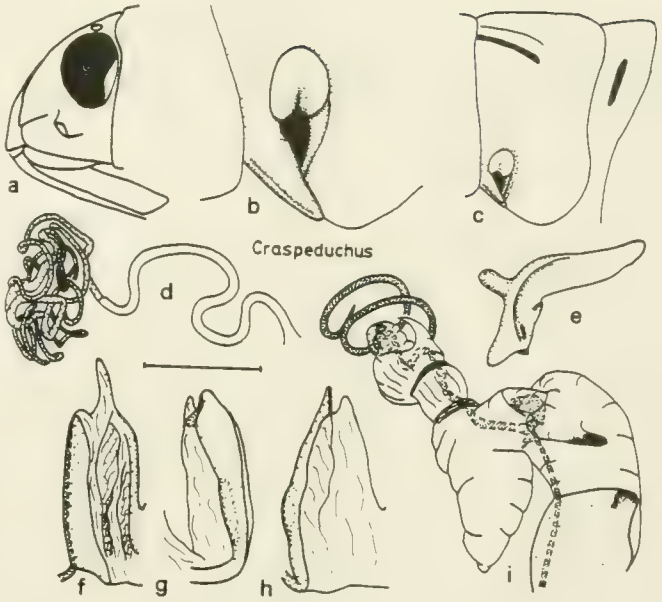


Fig. 5. *Craspeduchus xanthostaurus* (Herrich-Schäffer). a. Head. b. Ostiolar peritreme and evaporative area. c. Metapleuron. d. Spermatheca. e. Left clasper, right lateral view. f-h. Ovipositor, left valvula and connecting membrane: f, first valve, ventral view; g, second valve, lateral view; h, second valve, ventral view. i. Partially inflated aedeagus, left lateral view. Scale (mm): a,c = 1.0; b,d,f-i = 0.5; e = 0.375.

ramus reaching almost to apex; second valve (figs. 5g,h) with connecting membrane unpigmented, without sclerotization, extending about to apex of valvula, cleft to about half distance from base, valvula flattened. *COLOR.* — *Head* black except small round spot on vertex pale yellow or purple, jugum occasionally dark purple, buccula pale yellow. *Pronotum* dark brown to black either with anterior lobe yellow or orange or with margins, narrowest at humeri, and a narrow longitudinal median line from anterior to posterior margins orange or pale yellow. *Scutellum* dark brown to black except sometimes apex pale. *Hemelytron* with margins of coriaceous part orange or pale yellow; membrane dark brown with narrow white apical margin. *Thoracic pleura* dark brown or purple to black except anterior margin of propleuron, all acetabulae, and posterior margins pale yellow. *Abdomen* with sterna II to VI bright orange red or brown suffused with orange, sternum VII and genital segments dark brown to black.

DISTRIBUTION. Species of *Craspeduchus* occur from southern Brazil to Panama. There is considerable overlap in the ranges of several species.

COMMENTS. Species of *Craspeduchus* are so similar to those of *Ochrostomus* in external structure that the two genera can be reliably separated only on color characters. They differ greatly in both male and female genitalia, and are, in fact, not closely related (see phylogenetic analysis).

KEY TO SPECIES OF *CRASPEDUCHUS* STÅL

1. Posterior pronotal lobe completely black 2
—Posterior pronotal lobe with margins and longitudinal median line red or yellow 3
2. Pronotum orange anteriorly, this color extending posterior to callar impressions ..... *buenoi*
—Pronotum yellow anteriorly, this color not extending posterior to callar impressions ..... *variegatus*
3. Pronotum with lateral and posterior margins and median longitudinal line red; clavus entirely yellow ..... *matudai*
—Pronotum with lateral and posterior margins and median longitudinal line yellow; clavus at least partly black 4
4. Claval suture red; margin of clavus adjacent to scutellum black ..... *circumseptus*

—Claval suture black; margin of clavus adjacent to scutellum yellow 5
5. Lateral margins of abdominal sterna red ..... *xanthostaurus*
—Lateral margins of abdominal sterna black ..... *nigrolimbatus*

Dalmochrimnus Brailovsky
(Fig. 6)

Dalmochrimnus Brailovsky, 1982a: 138. Type species: *Lygaeus* (*Ochrostomus*) *plagiatus* Distant, 1882, monobasic.
Malleochrimnus Brailovsky, 1982a: 140. Type species: *Lygaeus* (*Ochrostomus*) *guatemalanus* Distant, 1882. **n. syn.**

Included species: *Dalmochrimnus ayalai* (Brailovsky), 1984d (*Malleochrimnus*), **n. comb.**; *Dalmochrimnus circumplicatus* (Distant), 1882 (*Lygaeus* (*Melanocoryphus*)), **n. comb.**; *Dalmochrimnus defessus* (Van Duzee), 1929 (*Lygaeus* (*Craspeduchus*)), **n. comb.**; *Dalmochrimnus guatemalanus* (Distant), 1882 (*Lygaeus* (*Ochrostomus*)), **n. comb.**; *Dalmochrimnus nigriguttulus* (Stål), 1874 (*Melanocoryphus*) = *Neacoryphus pelaezi* Brailovsky, 1977a, fide Brailovsky, 1984b = *Neacoryphus splendidus* Brailovsky, 1977b, fide Brailovsky, 1984b; *Dalmochrimnus plagiatus* (Distant) 1882 (*Lygaeus* (*Ochrostomus*)); *Dalmochrimnus prominens* (Brailovsky) 1984d (*Malleochrimnus*), **n. comb.**

BODY. Robust; impunctate except pronotum immediately in front of and behind callus; hairs moderately long, curved, dense, moderately coarse and semiupright dorsally, finer and decumbent ventrally, densest on head, pronotum, and scutellum. Length 7.5-10.0mm. *Head* (fig. 6a) moderately declivent; vertex strongly convex; ocellus distinctly raised above surface mesally and posteriorly, distance between ocelli about six times distance from ocellus to eye; buccula slightly produced, ventral margin slightly convex. *Pronotum* with posterior width slightly less than twice anterior width; medial length slightly greater than anterior width; anterior margin concave, raised, beaded laterally, separated from callus by depressed, indistinctly punctate area; posterior margin sinuate, slightly convex medially, convex and slightly produced posteriad to either side of scutellum; lateral margins almost straight, slightly convex posteriorly; callus distinct, callar impressions unbranched, oblique, slightly curved; postcallar impression deep immediately behind callus, extending well onto disc of posterior lobe to give impression that lateral margins are swollen, a few coarse punctures anteriorly, impunctate posteriorly, interrupted medially and to either side of midline by distinct carinae. *Scutellum* with length about 0.75 times width; stem and arms of median carina about equally broad; lateral fovea deep anteriorly, becoming shallow and less distinct posteriorly, bottom smooth. *Hemelytron* surpassing apex of abdomen; corial veins indistinct, slightly raised. *Propleuron* divided into three parts by distinct dorsoventral impressions, a few indistinct punctures on anterior part and along posterior impression, median part slightly convex. *Mesopleuron* divided into anterior and posterior sections by indistinct dorsoventral impression, a few indistinct punctures along impression. *Metapleuron* (fig. 6c) impunctate; posterior margin directed slightly anterodorsally, straight or slightly concave, posterior margin of acetabula not produced posteriorly; ostiolar peritreme (fig. 6b) with anterior margin of channel higher than posterior margin, apical button rounded, distinct from surrounding pleuron dorsally and posteriorly; evaporative area small, surrounding dorsal part of peritreme. *Abdomen* without anterolateral scars; sternum II fully exposed; sternum VI of female about two-thirds as long medially as laterally; sternum VII of female cleft to base. *GENITALIA.* — *Clasper* (fig. 6h) with blade at right angle to shank, about as long as shank, curved, somewhat dorsoventrally flattened, twisted so that inner face is somewhat ventrally directed; posterior projection well developed, somewhat dorsally directed, thin, conical; shank without rooflike interior projection, a curved longitudinal posterior ridge on inner face not extending onto base of blade, inner face anterior of ridge flattened or with shallow groove, an indistinct anterior ridge near junction with blade. *Aedeagus* (fig. 6i) bent before telescoping into phallotheca; conjunctiva short with large, slightly crescent-shaped, subapical, lateral lobe armed densely with small spines apically, without dorsal subapical lobe; vesica fairly symmetrically swollen proximad and distad of ring sclerite, without projections distad of ring sclerite; ring sclerite well developed, without projections; gonoporal process elongate, robust; apical process of secondary gonopore elongate, robust, almost closed dorsally to form secondary tube; phallotheca with ridge along almost entire apical margin, apical part of disc with at least two dorsolaterally directed flanges, process short, flared laterally. *Spermatheca* (fig. 6d) with long basal tube; apical tube broad basally, becoming rapidly thinner, complexly coiled, heavily pigmented; apical bulb elongate, narrow, complexly coiled, not differentiated from adjacent tube. *Ovipositor* short, moderately broad; first valve (fig. 6e) with connecting membrane extending beyond apex of valvula about one-third valvular length, cleft medially almost to base, a secondary cleft laterad resulting in a shoulder at about level of apex of valvula medially and a longer projection laterally, Y-sclerite distinct, stem short, arms reaching level of apex of membrane but interrupted at lateral cleft, valvifer triangular, valvula triangular, ramus almost reaching apex; second valve (figs. 6f,g) with connecting membrane cleft almost to base, an acute projection at each side of cleft not reaching level of apex of valvula, a large subquadrate pigmented or sclerotized area on each side of cleft, valvula flattened except for an elongate subapical swelling along posterior margin. *COLOR.* — *Head* black, either with or without pale spot on vertex. *Pronotum* usually red on margins with black macula occupying most of disc of anterior lobe and at least part of disc of posterior lobe. *Scutellum* dark brown to black except sometimes extreme apex pale orange or red. *Hemelytron* usually dark centrally with pale margins, occasionally completely red; membrane dark brown to black, without or with extremely narrow white apical margin. *Thoracic pleura* dark except pale margins of varying width. *Abdomen* ventrally with segment VII and genital segments black, otherwise either entirely orange or red or black with orange or red markings.

DISTRIBUTION. Six of the seven species occur from Baja Cali-

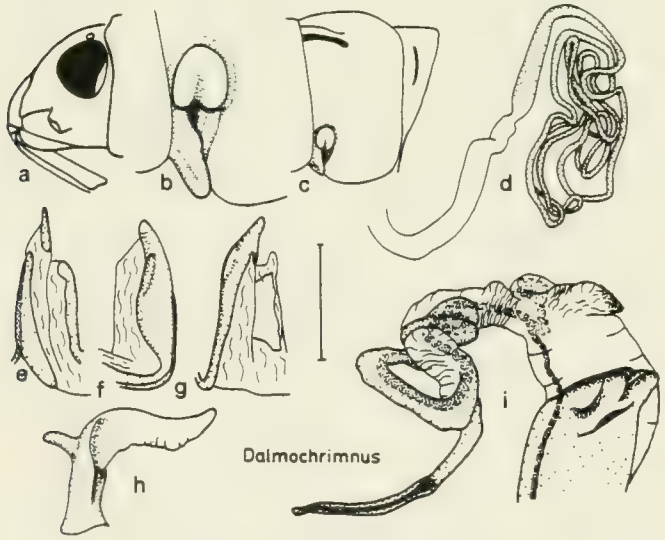


Fig. 6. *Dalmochrimnus nigriguttulus* (Stål). a. Head. b. Ostiolar peritreme and evaporative area. c. Metapleuron. d. Spermatheca. e-g. Ovipositor, left valvula and connecting membrane: e, first valve, ventral view; f, second valve, lateral view; g, second valve, ventral view. h. Left clasper, right lateral view. i. Partially inflated aedeagus, left lateral view. Scale (mm): a,c = 1.0; b, d-g,i = 0.5; h = 0.375.

fornia to Costa Rica with considerable overlap in their ranges. One species is restricted to northern South America.

COMMENTS. The combination of dense dorsal pubescence and flattened pronotum is diagnostic for *Dalmochrimnus*. Brailovsky divided species treated here as *Dalmochrimnus* between his genera *Dalmochrimnus* and *Malleochrimnus* based on the presence or absence of the pale spot on the vertex. As this character has been found to be variable within other genera, and both male and female genitalia are of a single general type, I have combined them here.

KEY TO SPECIES OF *DALMOCHRIMNUS* BRAILOVSKY

1. Head completely black dorsally 2
—Head with a small pale spot at vertex 4
2. Abdominal sterna III-VI entirely or predominantly red or orange 3
—Abdominal sterna III-VI predominantly black ..... *plagiatus*
3. Abdominal sterna III-VI entirely orange or red ..... *nigriguttulus*
—Abdominal sterna III-VI with transverse black lines laterally ..... *circumplicatus*
4. Apical margin of corium black 5
—Apical margin of corium orange or yellow 6
5. Longitudinal median pale line of pronotum narrow, not reaching anterior margin ..... *defessus*
—Longitudinal pale line of pronotum broad, especially posteriorly, reaching anterior margin ..... *guatemalanus*
6. Acetabulae almost entirely yellow ..... *prominens*
—Acetabulae with only narrow margins yellow ..... *ayalai*

Ektyphonotus new genus
(Fig. 7)

Type species: *Lygaeus* (*Ochrostomus*) *cruentatus* Distant, 1882.

Included species: *Ektyphonotus cruentatus* Distant, 1882 (*Lygaeus* (*Ochrostomus*)).

BODY. Moderately robust; impunctate except pronotum immediately before and behind callus, indistinctly on prosternum, and on propleura and mesopleura; hairs short, fine, decumbent, moderately dense, slightly denser on abdominal venter. Length 7.0-7.5mm. *Head* (fig. 7a) strongly declivent; vertex slightly convex; ocellus distinctly raised above surface mesally and posteriorly, distance between ocelli about five times distance from ocellus to eye; buccula strongly produced, ventral margin strongly convex. *Pronotum* with posterior width slightly less than twice anterior width; medial length slightly greater than anterior width; anterior margin concave, raised, beaded laterally, separated from callus by slightly depressed area bearing scattered fine punctures; posterior margin convex; lateral margins almost straight, slightly convex anteriorly and posteriorly, slightly indented behind callus; callus indistinct, callar impressions unbranched, transverse medially, curving toward anterior angles laterally; very shallow uninterrupted impression with fine, shallow punctation just posterior to callus; median carina obsolete. *Scutellum* with length about 0.8 times width; stem and arms of median carina broad; lateral fovea shallow, indistinct posteriorly, bottom rugose. *Hemelytron* surpassing apex of abdomen; corial veins indistinct, slightly raised; membrane opaque. *Propleuron* divided into three parts by dorsoventral impressions, anterior and posterior parts indistinctly punctate, median part slightly convex. *Mesopleuron* divided into anterior and posterior sections by dorsoventral impression, posterior part indistinctly punctate. *Metapleuron* (fig. 7c) impunctate; posterior margin directed slightly anterolaterally, slightly convex, posterior margin of acetabula slightly produced posteriorly; ostiolar peritreme (fig. 7b) with anterior margin higher than posterior margin, apical button rounded, distinctly separated from surrounding pleuron dorsally and posteriorly; evaporative area small, surrounding dorsal part of peritreme. *Abdomen* without anterolateral scars; sternum II fully exposed; sternum VI of female about two-thirds as long medially as laterally; sternum VII of female cleft to base. *GENITALIA.* — *Clasper* (fig. 7i) with blade at right angle to shank, moderately curved, somewhat dorsoventrally flattened, posterior projection subconical, moderately developed, shank with rooflike interior projection, posterior and median longitudinal ridges on inner face projecting most strongly just below level of posterior projection, lower margin of blade with projection near base. *Aedeagus* (fig. 7d) bent before telescoping into phallotheca; conjunctiva short, without subapical lobes; vesica strongly, asymmetrically produced laterally proximad of ring sclerite, without projections distad of ring sclerite; ring sclerite small, without projections; gonoporal process moderately elongate, robust; apical process of secondary gonopore broad, blunt; phallotheca without apical flange, a small rugose area on disc, process short with ridge along proximal margin. *Spermatheca* (fig. 7h) with short broad basal tube, apical tube moderately elongate, unpigmented except just basad of apical bulb, apical bulb tubular, complexly coiled, not differentiated from adjacent tube. *Ovipositor* moderately elongate; first valve (fig. 7e) with connecting membrane extending beyond apex of valvula about one-third valvular length, cleft to about one-fourth distance to base, Y-sclerite distinct, small, stem very short, arms extending about half

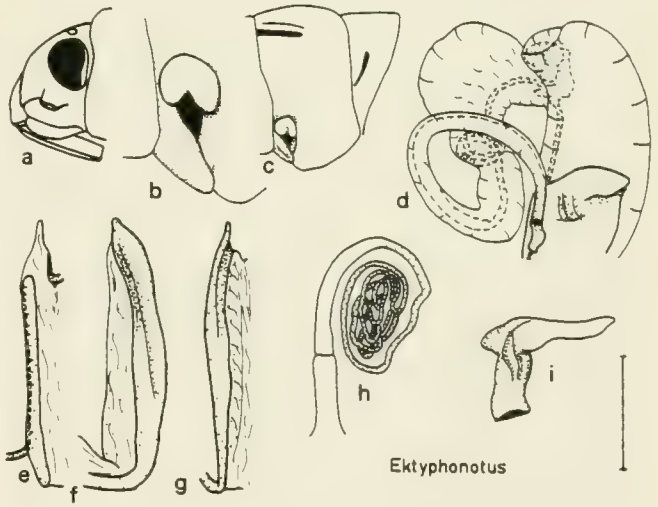


Fig. 7. *Ektyphonotus cruentatus* (Distant). a. Head. b. Ostiolar peritreme and evaporative area. c. Metapleuron. d. Partially inflated aedeagus, left lateral view. e-g. Ovipositor, left valvula and connecting membrane: e, first valve, ventral view; f, second valve, lateral view; g, second valve, ventral view. h. Spermatheca. i. Left clasper, right lateral view. Scale (mm): a,c = 1.0; b,e-h = 0.5; d,i = 0.375.

distance from base of cleft to apex of membrane; second valve (figs. 7f,g) with connecting membrane only slightly cleft medially, with small shoulder at each side of cleft, valvula swollen longitudinally along ventral margin subapically, flattened along dorsal margin. *COLOR.* — Dull brown and pale yellow, occasionally with orange tints. *Head* pale, infuscate medially, darkest on tylus and behind ocelli, faint pale spot on vertex; bucculae pale. *Pronotum* with margins and broad longitudinal median line pale, anterior lobe otherwise reddish, posterior lobe otherwise brown. *Scutellum* brown with broad longitudinal median line pale yellow. *Hemelytron* with clavus and corium brown except pale costal margin of corium and claval commissure; membrane brown, lighter along margins laterally and with a yellowish longitudinal median line from base almost to apex, without distinct white apical or lateral margins. *Thoracic pleura* pale, often infuscate medially, propleuron sometimes reddish medially. *Abdomen* ventrally pale except infuscate lateral longitudinal line, line broadest basally, becoming obsolete apically.

DISTRIBUTION. The single species occurs from Panama to southeastern Brazil.

COMMENTS. The name *Ektyphonotus* is from the Greek and refers to the swollen appearance of the pronotum.

Brailovsky (1983b) included *E. cruentatus* in the "*poeyi* group" of his genus *Torvochrimnus*, which included the type species of that genus. Externally *E. cruentatus* differs from the species of *Torvochrimnus* in its more slender body shape; in the shape of the pronotum, which is more strongly tapered anteriorly and higher posteriorly; and in coloration. The shape of the apical process of the secondary gonopore, lack of distinct aedeagal lobes, and elongate ovipositor with shallow median cleft and distinct Y-sclerite are diagnostic for the genus.

Hadrosomus new genus
(Fig. 8)

Type species: *Lygaeus teapensis* Distant, 1893.

Included species: *Hadrosomus confraternus* (Uhler), 1869 (*Lygaeus*) = *Lygaeus modestus* Stål, 1858, preocc. fide Slater, 1964a = *Ochrostomus neomodestus* Slater, 1964a, fide Froeschner, 1979; *Hadrosomus corallipes* (Brailovsky), 1983b (*Torvochrimnus*); *Hadrosomus teapensis* (Distant), 1893 (*Lygaeus*).

BODY. Robust; impunctate except indistinctly on pronotum before and behind callus and on thoracic pleura; hairs sparse on disc of pronotum, moderately dense on hemelytron, densest on abdominal venter, short, fine, semidecumbent, interspersed with a few longer upright hairs medially on abdominal venter. Length 9.0-11.5mm. *Head* (fig. 8a) moderately declivent, vertex moderately convex; ocellus slightly raised above surface mesally and posteriorly, directed anterolaterally, distance between ocelli about seven times distance from ocellus to eye; buccula moderately to strongly produced, ventral margin moderately to strongly convex. *Pronotum* with posterior width about twice anterior width; medial length slightly greater than anterior width; anterior margin raised, most distinctly laterally, not beaded, separated from callus by shallow, punctate depression; posterior margin slightly convex; lateral margins almost straight anteriorly, tumid and slightly convex posteriorly; callus low, distinct, callar impressions branched, slightly curved, slightly sinuate; postcallar impression shallow, indistinctly punctate, not reaching lateral margin, interrupted medially by indistinct carina; disc of posterior lobe convex, slightly higher than lateral margins, flattening laterally. *Scutellum* with length about 0.8 times width; stem and arms of median carina broad, stem becoming lower apically; lateral fovea becoming indistinct apically, bottom smooth. *Hemelytron* considerably surpassing apex of abdomen; corial veins distinct, distinctly raised; membrane opaque. *Propleuron* divided into three parts by shallow dorsoventral impressions; impressions with shallow punctation. *Mesopleuron* divided into two parts by indistinct dorsoventral impression; with shallow punctation posteriorly. *Metapleuron* (fig. 8c) impunctate; posterior margin directed slightly posteroventrally, slightly convex, posterior margin of acetabula not produced posteriorly; ostiolar peritreme (fig. 8b) with anterior margin of channel slightly higher

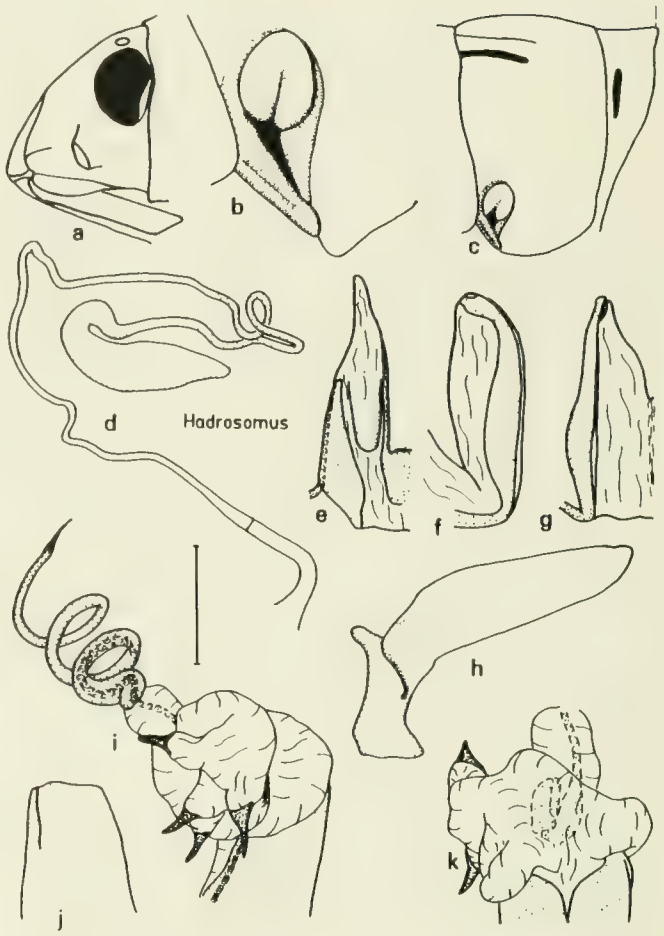


Fig. 8 *Hadrosomus teapensis* (Distant). a. Head. b. Ostiolar peritreme and evaporative area. c. Metapleuron. d. Spermatheca. e-g. Ovipositor, left valvula and connecting membrane: e, first valve, ventral view; f, second valve, lateral view; g, second valve, ventral view. h. Left clasper, right lateral view. i-k. Partially inflated aedeagus: i, left lateral view; j, phallotheca, left lateral view; k, dorsal view. Scale (mm): a,c = 1.0; b,d-g, i-k = 0.5; h = 0.375.

than posterior margin, apical button ovate, distinctly separated from surrounding pleuron dorsally and posteriorly; evaporative area small, surrounding dorsal part of peritreme. *Abdomen* without anterolateral scars; sternum II fully exposed; sternum VI of female about two-thirds as long medially as laterally; sternum VII of female cleft to base. *GENITALIA.* — *Clasper* (fig. 8h) with blade at oblique angle to shank, broad dorsoventrally, flattened, only slightly curved inward, twisted dorsoventrally, a distinct or indistinct tooth on ventral margin at junction with shank; shank much shorter than blade, without rooflike interior projection, ridge from about midpoint near anterior margin extending obliquely posteriad to connect with dorsal margin of blade; posterior projection distinct, thumblike. *Aedeagus* (figs. 8i-k) bent before telescoping into phallotheca; conjunctiva short, strongly, irregularly swollen apically, subapical lateral lobes bifid, armed with single apical spines; vesica small, without distinct lobes or spines; ring sclerite elongate, extending around first coil of gonoporal process; apical process of secondary gonopore short, acute, and very slender at apex; phallotheca with opening almost ventral, process concave with apical ridge. *Spermatheca* (fig. 8d) with short moderately broad basal tube; apical tube long, thin, pigmented apically, apical bulb elongate, apex acute, base bent sharply. *Ovipositor* short; first valve (fig. 8e) with connecting membrane extending beyond

apex of valvula by about length of valvula, cleft to about one-third distance from base, Y-sclerite distinct, stem broad, arms not reaching apex of membrane, an ovate sclerite between Y-sclerite and valvula, less distinct apically; second valve (figs. 8f,g) with connecting membrane cleft to about half distance from base, an ill-defined subapical projection at each side of cleft, valvula flattened. *COLOR.* — Variously colored in yellows and browns often suffused with reddish tones. *Head* pale except dark brown to black around tylus and ocelli. *Pronotum* either completely pale except callar impressions or broadly infuscated laterad of midline. *Scutellum* brown with pale median line. *Hemelytron* light to dark brown with contrasting pale veins; membrane pale brown to white with veins contrasting dark brown, without or with very narrow white apical margin. *Thoracic pleura* light yellow or brown, sometimes with linear black markings. *Abdomen* ventrally pale brown or yellow, sometimes with narrow transverse black markings.

DISTRIBUTION. Hadrosomus confraternus occurs from south-central Mexico to southern Brazil. *H. teapensis* is apparently restricted to the southern half of Mexico, where its range overlaps broadly with that of *H. confraternus*. The third species, *H. corallipes*, is known only from "Caracas, Brasil", a locality I have been unable to locate.

COMMENTS. The name *Hadrosomus* is from the Greek and refers to the robust body. *Hadrosomus* species are very similar in general appearance to *Biblochrimnus* species. They may be easily separated by their smaller size, less declivent pronotum, and the contrasting coloration of the hemelytral veins. The deeply cleft second ovipositor valve, without median sclerite, further separates them from members of that genus.

KEY TO SPECIES OF *HADROSOMUS*

1. Scent gland orifice red; legs entirely black.....*corallipes*
—Scent gland orifice yellow; legs not entirely black 2
2. Head predominantly reddish, black anterior mark covering most of apex.....*teapensis*
—Head predominantly yellow or ocher, black anterior mark restricted to tylus or nearly so .....*confraternus*

Latochrimnus Brailovsky
(Fig. 9)

Latochrimnus Brailovsky, 1982a: 141. Type species: *Lygaeus vittiscutis* Stål, 1862, monobasic.

Included species: *Latochrimnus aduncus* Brailovsky, 1984c; *Latochrimnus badilloi* Brailovsky, 1984c; *Latochrimnus funereus* Brailovsky, 1984c; *Latochrimnus nigraosteolaris* Brailovsky, 1984c; *Latochrimnus vittiscutis* (Stål), 1862 (*Lygaeus*).

BODY. Moderately robust; impunctate except pronotum immediately before and behind callus and on prosternum and pro- and mesopleura; hairs fine, of moderate length, decumbent, moderately dense dorsally, slightly denser on abdominal venter. Length 4.5-6.0mm. *Head* (fig. 9a) moderately declivent; vertex only slightly convex; ocellus distinctly raised above surface mesally and posteriorly, distance between ocelli about seven times distance from ocellus to eye; buccula slightly produced, ventral margin moderately convex. *Pronotum* with posterior width about 1.7 times anterior width; medial length slightly greater than anterior width; anterior margin concave, raised, sometimes beaded laterally, separated from callus by coarsely punctate area; posterior margin very slightly convex; lateral margins almost straight, very slightly convex anteriorly and posteriorly, very slightly indented behind callus; callus distinct, callar impressions unbranched, sinuate, oblique; shallow impression behind callus extending over about anterior half of posterior lobe, deeply punctate just posterior to callus, punctures becoming less dense and deep posteriorly, interrupted medially by distinct carina. *Scutellum* with length about 0.7 times width; stem of median carina much lower than arms; lateral fovea distinct posteriorly, bottom rugose. *Hemelytron* surpassing apex of abdomen; corial veins indistinct especially apically. *Propleuron* divided into three parts by dorsoventral impressions, anterior part strongly punctate, posterior part less so, median part impunctate and slightly convex. *Mesopleuron* divided into anterior and posterior sections by dorsoventral impression, posterior part punctate. *Metapleuron* (fig. 9c) impunctate; posterior margin directed slightly anterolaterally, straight or slightly convex, posterior margin of acetabula not produced posteriorly; ostiolar peritreme (fig. 9b) with anterior margin of channel higher than posterior margin; apical button rounded, distinctly separated from surrounding pleuron dorsally and posteriorly; evaporative area small, surrounding dorsal part of peritreme. *Abdomen* without anterolateral scars; sternum II fully exposed; sternum VI of female about two-thirds as long medially as laterally; sternum VII of female cleft to base. *GENITALIA.* — *Clasper* (fig. 9h) with blade at about right angle to shank, about as long as shank, curved, flattened, twisted so that inner face is somewhat ventrally directed; posterior projection thin, thumblike, somewhat dorsally directed; shank with low rooflike interior projection, a low carina present near juncture with blade. *Aedeagus* (figs. 9i,j) bent before telescoping into phallotheca; conjunctiva short, with somewhat crescent-shaped subapical lobes armed with single apical spine; vesica somewhat asymmetrically swollen proximad of ring sclerite, symmetrically swollen distad of ring sclerite; ring sclerite narrow, with small apical projection; gonoporal process moderately elongate, apical process of secondary gonopore short, spoon-shaped. *Spermatheca* (fig. 9g) with basal tube elongate, without swelling; apical tube short, slender, irregularly coiled; apical bulb short, globular, blunt apically. *Ovipositor* short, moderately broad; first valve (fig. 9d) with connecting membrane cleft to about one-fourth distance from base, extending beyond apex of valvula by about half length of valvula, no distinct Y-sclerite but light pigmentation near cleft, valvifer triangular, valvula subtriangular, ramus almost reaching apex; second valve (figs. 9e,f) with connecting membrane cleft to about one-third distance from base, without projections, a small pigmented area at each side of base of cleft, valvula flattened. *COLOR.* — Colors often washed out, sometimes distinct, dark markings brown, light markings pale yellow or orange. *Head* dark at least around eyes and on tylus, with or without pale spot on vertex; bucculae pale. *Pronotum* pale with dark lateral maculae of varying shape and distinctness on posterior lobe. *Scutellum* dark except stem of median carina pale. *Hemelytron* dark except costal and apical corial margins and claval commissure pale, width of pale areas variable; membrane dark ex-

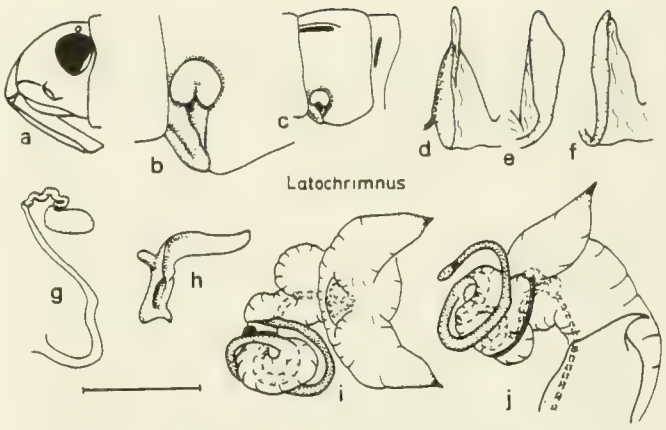


Fig. 9. *Latochrimnus vittiscutis* (Stål). a. Head. b. Ostiolar peritreme and evaporative area. c. Metapleuron. d-f. Ovipositor, left valvula and connecting membrane: d, first valve, ventral view; e, second valve, lateral view; f, second valve, ventral view. g. Spermatheca. h. Left clasper, right lateral view. i,j. Aedeagus: i, dorsal view; j, left lateral view. Scale (mm): a,c = 1.0; b,d-g = 0.5; h-j = 0.375.

cept for distinct, narrow, regular, white margin laterally and apically. *Thoracic pleura* dark except margins pale, peritreme usually pale, occasionally black. *Abdomen* of female pale medially, dark laterally, of male dark, sternum VII and genital segments always dark.

DISTRIBUTION. Two species range from Mexico to Costa Rica, one species from Panama to northern South America, one species is restricted northern South America, and one species is known only from southern Brazil.

COMMENTS. The best external character for identification of *Latochrimnus* is the moderately dense dorsal pubescence. Identification of species is best based on examination of male genitalia as the color characters used in the key are somewhat variable.

KEY TO SPECIES OF *LATOCHRIMNUS* BRAILOVSKY

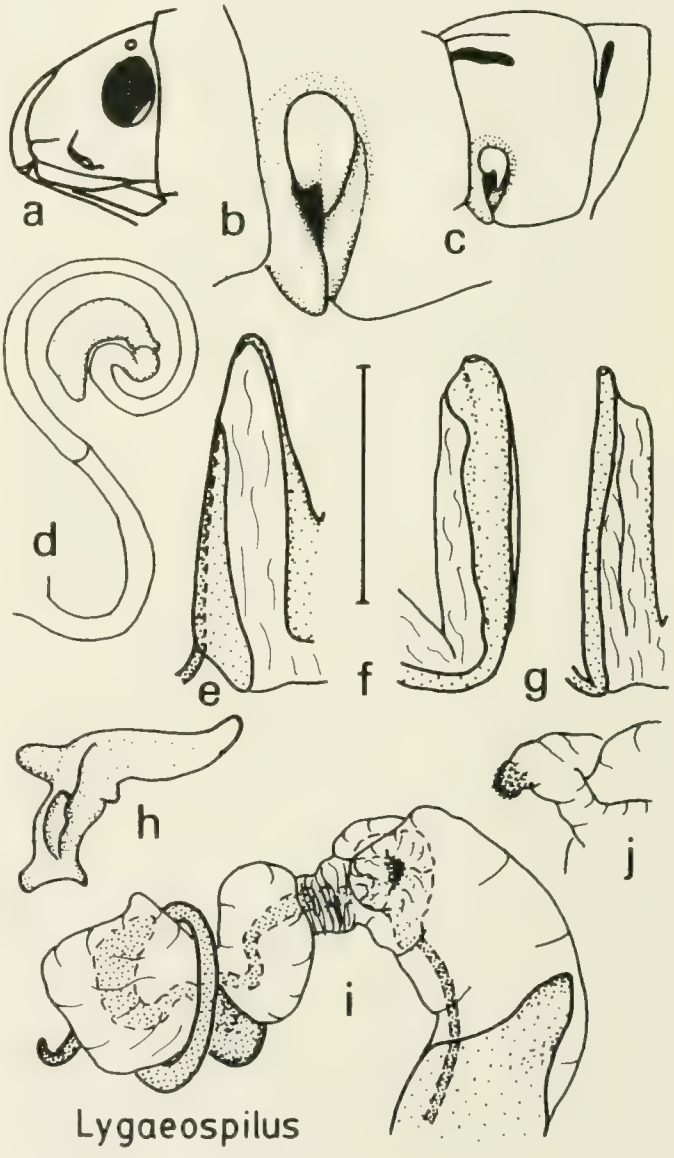
1. Costal margin of corium yellow or orange at base and apex, dark medially; dark pronotal maculae covering humeral angles 2
—Costal margin of corium completely yellow orange; dark pronotal maculae not covering humeral angles 3
2. Dorsum of head pale laterally; scutellum with a pale longitudinal median line.....*aduncus*
—Dorsum of head completely dark; scutellum pale only at apex .....*badilloi*
3. Ostiolar peritreme black.....*nigraosteolaris*
—Ostiolar peritreme pale orange or yellow 4
4. Rostrum reaching posterior margin of metacoxa, segment I scarcely surpassing anterior prosternal margin, anterior pronotal lobe with more or less distinct dark markings laterad of midline .....*funereus*
—Rostrum reaching at least basal 1/3 of abdominal sternum III, segment I extending about 1/3 its length beyond anterior prosternal margin; anterior pronotal lobe with at most faint infuscation to either side of midline .....*vittiscutis*

Lygaeospilus Barber
(Fig. 10)

Lygaeus (*Lygaeospilus*) Barber, 1921: 65, 68. Type species: *Aphanus tripunctatus* Dallas, 1852, monobasic.
Lygaeospilus Barber, 1948: 67.

Included species: *Lygaeospilus brevipilus* Scudder, 1981; *Lygaeospilus fusconervosus* Barber, 1948; *Lygaeospilus pusio* (Stål), 1874 (*Melanocoryphus*) = *Lygaeus albulus* Distant, 1893, fide Barber, 1921 = *Lygaeosoma solida* Uhler, 1893, fide Van Duzee, 1909; *Lygaeospilus tripunctatus* (Dallas), 1852 (*Aphanus*) = *Melanocoryphus* (*Melanocoryphus*) *obscuripennis* Stål, 1874, fide Barber, 1921.

BODY. Moderately robust; impunctate except pronotum before and behind callus and on prosternum and pro- and mesopleura; hairs sparse dorsally, denser on abdominal venter, short decumbent hairs interspersed with long upright hairs. Length 4.0-5.5mm. *Head* (fig. 10a) moderately declivent; vertex strongly convex; ocellus distinctly raised above surface mesally and posteriorly, distance between ocelli about seven times distance from ocellus to eye; buccula moderately produced, ventral margin moderately convex. *Pronotum* with posterior width about 1.5 times anterior width; medial length slightly less than anterior width; anterior margin concave, raised, most distinctly raised laterally, not beaded, separated from callus by deeply punctate depression; posterior margin slightly sinuate; lateral margins almost straight, slightly convex adjacent to callus; callus distinct, callar impressions unbranched, strongly oblique, slightly sinuate; shallow impression behind callus extending over about anterior half of posterior lobe, deeply punctate just posterior to callus, interrupted medially by distinct carina. *Scutellum* with length about 0.8 times width; stem and arms of median carina broad; lateral fovea distinct posteriorly, bottom smooth. *Hemelytron* often not reaching apex of abdomen; corial veins distinct, moderately raised; membrane opaque. *Propleuron* divided into three parts by dorsoventral impressions, anterior and posterior parts flat and strongly punctate, median part convex and impunctate. *Mesopleuron* divided into anterior and posterior sections by dorsoventral impression, posterior part weakly punctate. *Metapleuron* (fig. 10c) impunctate; posterior margin directed dorsoventrally, convex, posterior margin of acetabula not produced posteriorly; ostiolar peritreme (fig. 10b) with anterior margin of channel higher than posterior margin; apical button ovate with long axis dorsoventral, distinctly separated from surrounding pleuron dorsally and posteriorly; evaporative area small, surrounding dorsal part of peritreme. *Abdomen* without anterolateral scars; sternum II fully exposed; sternum VI of female about half as long medially as laterally; sternum VII of female cleft to base. *GENITALIA.* — *Clasper* (fig. 10h) with blade almost at right angle to shank, strongly curved, flattened horizontally, posterior pro-



jection conical, well developed, shank with rooflike interior projection near junction with blade, basad of projection two longitudinal ridges separated by a distinct groove, short ridge at angle formed by junction of shank and blade. *Aedeagus* (figs. 10i,j) bent before telescoping into phallotheca; conjunctiva moderately elongate with bluntly pointed subapical lateral lobes armed with several minute spines; vesica proximad of ring sclerite fairly symmetrically swollen, without lobes or spines, distad of ring sclerite somewhat asymmetrically swollen, with small, membranous, subapical projection; ring sclerite well developed, without extensions; gonoporal process moderately elongate, robust; apical process of secondary gonopore short, acute; phallothecal process protruding, flared laterally. *Spermatheca* (fig. 10d) with basal tube of moderate length, thick, without swelling; apical tube pigmented apically, about as thick as basal tube basally, becoming coiled and slightly thinner than basal tube just basad of apical bulb; apical bulb somewhat elongate and irregular in outline, apex usually subacute. *Ovipositor* moderately elongate; first valve (fig. 10e) with connecting membrane extending beyond apex of valvula about half length of valvula, cleft to about half distance from apex to base, Y-sclerite completely surrounding cleft and extending slightly around membrane apex; second valve (figs. 10f,g) with connecting membrane cleft almost to base, edges of cleft heavily pigmented, with distinct shoulder but no projection near apex of cleft, valvula slightly convex. *COLOR.* — *Head* entirely black. *Pronotum* brown, reddish brown, or reddish, without distinct markings. *Scutellum* dark brown or reddish brown except sometimes apex and median carina pale. *Hemelytron* brown, reddish brown, or reddish, without distinct margins; membrane dark brown to black with apical margin and sometimes discal markings white. *Thoracic pleura* brown or reddish brown centrally, margins pale. *Abdomen* ventrally mottled with dark and pale brown and reddish brown.

DISTRIBUTION. Of the four recognized species, one is endemic to the Pacific northwest of the United States and Canada, one species is endemic to southern California, one species ranges from Guatemala to the southern United States, and one species occurs from southeastern Canada to central Mexico.

COMMENTS. Members of *Lygaeospilus* are very similar to those of *Melacoryphus* both externally and in the structure of male and female genitalia. It is quite possible that the differences found are a result of the smaller size of members of *Lygaeospilus*. If so, recognition of *Lygaeospilus* might leave *Melacoryphus* a paraphyletic group. It is also possible that *Lygaeospilus* is a polyphyletic genus composed of small species that, had they been larger, would have been placed in *Melacoryphus*.

KEY TO SPECIES OF *LYGAEOSPILUS* BARBER (SCUDDER, 1981)

1. Head, pronotum, and corium markedly pilose with both long, erect hairs and short semidecumbent hairs 2
—Head, pronotum, and corium not markedly pilose, having only short decumbent or semidecumbent hairs 3
2. Membrane distinctly margined with white; membrane with a central discoidal white spot; corium reddish ..... *pusio*
—Membrane fuscous with marginal area somewhat mottled and not with a distinct white border; center of membrane vaguely pale; corium fuscous ..... *tripunctatus*
3. Corium with decumbent sericeous hairs minute and very closely appressed; costal margin of corium distinctly and rather sharply convex in middle; second and third antennal segments thick and appearing robust; vertex width about equal to length of second antennal segment; scutellum length 1.8x commissure length in macropterous form; posterior part of pronotal disk weakly punctate ..... *brevipilus*
—Corium with decumbent sericeous hairs not minute and not very closely appressed; costal margin of corium straight or at most gently convex in middle; second and third antennal segments slender and not appearing robust; vertex width about equal to 0.75x length of second antennal segment; scutellum length 1.3x commissure length in macropterous form; posterior part of pronotal disc coarsely punctate ..... *fusconervosus*

Lygaeus Fabricius
(Fig. 11)

Lygaeus Fabricius, 1794: 133. Type species: *Cimex equestris* Linnaeus, 1758, designated by Curtis, 1833.
Eulygaeus Reuter, 1888: 550.

Included species (western hemisphere only): *Lygaeus alboornatus* Blanchard, 1852 = *Lygaeus albostillatus* Stål, 1858, fide Stål, 1874 = *Lygaeus albonotatus* (*sic*) Stål, 1868; *Lygaeus analis* Dallas, 1852 = *Lygaeus ruficeps* Stål, 1862, fide Distant 1901; *Lygaeus argutus* Brailovsky, 1982b, new name for *Lygaeus maculatus* Brailovsky, 1978b, preocc.; *Lygaeus ashlocki* Brailovsky, 1978b; *Lygaeus bahamensis* Barber & Ashlock, 1960; *Lygaeus coccineus* Barber, 1923 (*Lygaeus* (*?Melanostethus*)); *Lygaeus froeschneri* Brailovsky, 1978b; *Lygaeus inaequalis* Walker, 1872; *Lygaeus kalmii* Stål, 1874; *Lygaeus kalmii angustomarginatus* Parshley, 1919; *Lygaeus kalmii melanodermus* Montandon, 1893; *Lygaeus oppositus* Brailovsky, 1978b; *Lygaeus peruvianus* Brailovsky, 1978b; *Lygaeus reclivatus* Say, 1825 = *Lygaeus bipunctulus* Herrich-Schäffer, 1850, fide Dallas, 1852; *Lygaeus reclivatus enotus* Say, 1831 = *Lygaeus costalis* Herrich-Schäffer, 1843, fide Barber, 1921; *Lygaeus slateri* Gorski, 1968; *Lygaeus truculentus* Stål, 1862; *Lygaeus trux* Stål, 1862; *Lygaeus turcicus* Fabricius, 1803 = *Lygaeus trimaculatus* Dallas, 1852, fide Barber, 1921.

Incertae sedis species (western hemisphere only): *Lygaeus cognatus* Walker, 1872; *Cimex pubicornis* Fabricius, 1775; *Cimex scabrosus* Fabricius, 1775; *Cimex sexpustulatus* Fabricius, 1775; *Lygaeus signatus* Costa, 1862; *Lygaeus sipolisi* Fallou, 1891. SEE ADDENDUM.

BODY. Robust; impunctate except before and behind callus on pronotum and sparsely and indistinctly on prosternum and anterior third of propleuron; hairs short, decumbent, about equally dense dorsally and ventrally. Length 6.5-13.0mm. *Head* (fig. 11a) moderately declivent; vertex convex; ocellus slightly raised mesally and posteriorly, distance between ocelli about six times distance from ocellus to eye; buccula moderately to strongly produced, most strongly anteriorly, ventral margin slightly convex. *Pronotum* with posterior width about twice anterior width; medial length slightly greater than anterior width; anterior margin concave, slightly raised laterally, not beaded, separated from callus by shallow depression with coarse shallow punctation; posterior margin slightly concave medially, slightly convex laterally; lateral margins almost straight, slightly concave at anterior angles, slightly convex near humeri; callus indistinct, callar impressions branched at mesal ends, sinuate, angled toward anterior pronotal angles; depression behind callus shallow, with sparse coarse punctation, interrupted medially by low carina, not reaching lateral margins. *Scutellum* with length about 0.7-0.8 times width; arms of median carina broader than stem; lateral fovea distinct basally, becoming obsolete api-

← Fig. 10. *Lygaeospilus tripunctatus* (Dallas). a. Head. b. Ostiolar peritreme and evaporative area. c. Metapleuron. d. Spermatheca. e-g. Ovipositor, left valvula and connecting membrane: e, first valve, ventral view; f, second valve, lateral view; g, second valve, ventral view. h. Left clasper, right lateral view. i,j. Partially inflated aedeagus: i, left lateral view; j, left subapical lobe of conjunctiva, dorsal view. Scale (mm): a,c = 1.0; b,d-g 0.5; h-j = 0.375.

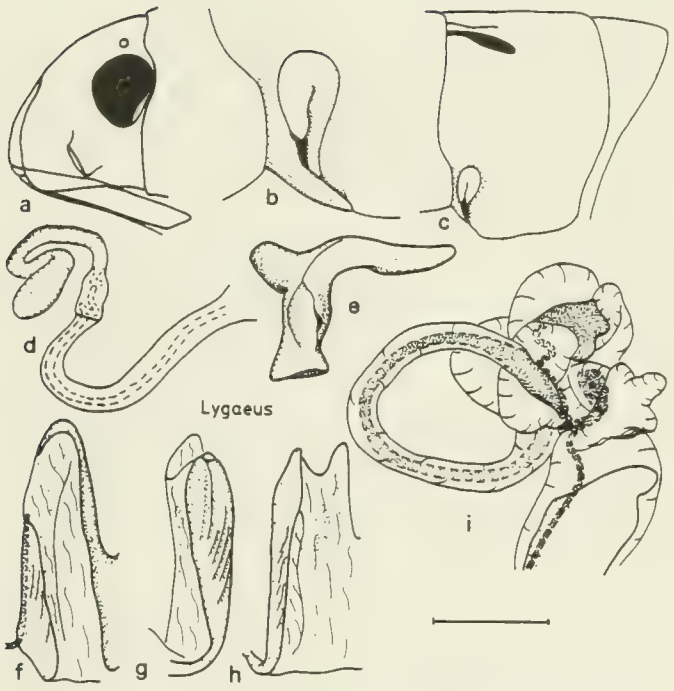


Fig. 11. *Lygaeus kalmii kalmii* Stål. a. Head. b. Ostiolar peritreme and evaporative area. c. Metapleuron. d. Spermatheca. e. Left clasper, right lateral view. f-h. Ovipositor, left valvula and connecting membrane: f, first valve, ventral view; g, second valve, lateral view; h, second valve, ventral view. i. Partially inflated aedeagus, left lateral view. Scale (mm): a,c = 1.0; b,d,f-i = 0.5; e = 0.375.

cally, bottom smooth. *Hemelytron* not or only slightly surpassing apex of abdomen; corial veins distinct, slightly raised; membrane opaque. *Propleuron* with postmedian dorsoventral impression, otherwise slightly convex, impunctate except for a few indistinct punctures in anterior third. *Mesopleuron* without noticeable dorsoventral impression, slightly convex, impunctate. *Metapleuron* (fig. 11c) impunctate; posterior margin directed dorsoventrally, convex, posterior margin of acetabula slightly produced posteriorly; ostiolar peritreme (fig. 11b) with anterior margin of channel slightly higher than posterior margin, apical button ovate with long axis dorsoventrally directed, without distinct separation from surrounding pleuron; evaporative area moderately large, surrounding apex of peritreme. *Abdomen* with comma-shaped anterolateral scars on sterna III-VII; sternum II fully exposed; sternum VI of female almost as long medially as laterally; sternum VII of female cleft to base. *GENITALIA. — Clasper* (fig. 11e) with blade at about right angle to shank, about as long as shank, curved, flattened, twisted so that inner face is somewhat ventrally directed; posterior projection long, often somewhat dorsally directed, either conical or thumblike; shank with posterior and median ridges on inner face separated by a shallow depression, joining dorsally to form a single ridge but usually not forming a rooflike projection, posterior ridge evenly convex, median ridge usually higher at one or both ends than in middle. *Aedeagus* (fig. 11i) bent before telescoping into phallotheca; conjunctiva short, with short, unarmed, dorsally directed, subapical, lateral lobes, without subapical dorsal lobe; vesica about equally asymmetrically swollen proximad and distad of ring sclerite, without distinct lobes or projections; ring sclerite well developed, heavily sclerotized; gonoporal process short, robust, covered by distinct membrane almost to apex; apical process of secondary gonopore very short, belled. *Spermatheca* (fig. 11d) with moderately elongate basal tube, swelling enclosing distinct coiled tube; apical tube short, moderately coiled; apical bulb large, irregularly globular. *Ovipositor* short; first valve (fig. 11f) with connecting membrane extending beyond apex of valvula by about length of valvula, cleft medially to about half distance to base, Y-sclerite distinct, extending around apex of membrane; second valve (figs. 11g,h) with connecting membrane cleft about half distance to base, a secondary cleft laterad of median cleft resulting in a small apical projection on each side of cleft, valvula with series of oblique grooves and ridges near middle, ventral margin slightly convex subapically. *COLOR. — Head* black except for longitudinal yellow or orange macula extending from vertex forward toward tylus and sometimes splitting anteriorly to reach jugum. *Pronotum* black in front of callus and to varying extent on disc of posterior lobe, otherwise red or orange. *Scutellum* black, occasionally apex reddish. *Hemelytron* red or orange with clavus sometimes partly or completely black, corium with black discal macula sometimes fused with subcostal black macula of varying size; membrane usually dark brown to black, rarely gray with contrasting darker veins or completely white, often with narrow apical margin, discal spot or spots, basal angle and digitiform macula from center of corial margin white. *Thoracic pleura* black except posterolateral margin of pronotum and occasionally center of all pleura red or orange. *Abdomen* with sterna II-VI red or orange with black maculae of varying extent medially and laterally, sternum VII and genital segments black.

DISTRIBUTION. Lygaeus species have been reported from all major regions except the Australian. The true distribution in the eastern hemisphere is uncertain due to confusion in generic placement of *Lygaeus* species and species of the closely related *Spilostethus* Stål. Of the 16 recognized western hemisphere species, one is endemic to the Bahama Islands, one is endemic to Puerto Rico, seven are restricted to South America (with the exception of a clearly introduced population of one species in Jamaica), one has been reported from the western United States south to northern South America, one is endemic to Mexico, one occurs from Mexico to Panama, and one occurs from the southwestern United States to southern Mexico. The distributions of the remaining three species are uncertain due to confusion about the proper names of the species in older literature.

COMMENTS. Lygaeus belongs to a mostly eastern hemisphere group of lygaeines characterized by the presence of dorsolateral abdominal scent gland openings. It is possible that recognition of the eastern hemisphere genus *Spilostethus* Stål leaves *Lygaeus* paraphyletic.

KEY TO WESTERN HEMISPHERE SPECIES OF *LYGAEUS* FABRICIUS

1. Head dorsally predominantly yellow or orange 2
—Head dorsally predominantly black, at most with a Y-shaped mark from vertex to in front of compound eye yellow or orange 6
2. Disc of hemelytral membrane without white markings 3
—Disc of hemelytral membrane with two ovate white maculae 4
3. Hemelytral membrane gray except veins contrasting dark brown to black; pale areas of pronotum and hemelytra pale orange to yellow ..... *inaequalis*
—Hemelytral membrane dark brown to black except white apical margin; pale areas of pronotum and hemelytra orange ..... *ashlocki*
4. Posterior margin of pronotum black laterally, pale medially; less than 8.5mm long ..... *slateri*

—Posterior margin of pronotum entirely black; more than 8.5mm long 5
5. Orange area anterior to posterior pronotal margin interrupted on either side of midline forming a central and two lateral maculae ..... *argutus*
—Orange area anterior to posterior pronotal margin not interrupted laterally ..... *analis*
6. Head dorsally with large Y-shaped orange or yellow mark extending from vertex to in front of eye 7
—Head dorsally with yellow or orange mark on vertex at most slightly bifid at anterior end 8
7. Corium with a small black macula on disc not or scarcely touching longitudinal black macula of costal margin ..... *trux*
—Corium without small black macula on disc, black macula of costal margin extending over disc ..... *turcicus*
8. Hemelytral membrane white 9
—Hemelytral membrane predominantly dark brown or grayish with contrasting dark brown veins 10
9. Pronotum black ..... *coccineus*
—Pronotum with orange markings on posterior lobe ..... *bahamensis*
10. Hemelytral membrane grayish with contrasting dark brown veins 11
—Hemelytral membrane dark brown except apical margin and sometimes one or two oval maculae on disc white 12
11. Corium with dark mark basally along claval suture and with dark mark along costal margin extensive ..... *truculentus*
—Corium with dark markings restricted to a small discal spot and a small macula at about middle of costal margin ..... *oppositus*
12. Hemelytral membrane without white markings on disc 13
—Hemelytral membrane with one or two oval white marks on disc 5
13. Clavus black ..... *kalmii angustomarginatus*
—At least anterior 1/3 of clavus orange 14
14. Corium with a small black macula on disc not or scarcely touching longitudinal black macula of costal margin ..... *trux*
—Corium with small black macula on disc confluent with black macula of costal margin ..... *reclivatus enotus*
15. Hemelytral membrane with one large round white mark on disc 16
—Hemelytral membrane with two white marks on disc 17
16. Pale markings of pronotum and hemelytra bright orange ..... *alboornatus*
—Pale markings of pronotum and hemelytra heavily infuscated, blackish ..... *froeschneri*
17. Clavus black 18
—At least anterior 1/3 of clavus red or orange 19
18. White discal maculae of hemelytral membrane distinct and regular in outline; western half of North America ..... *kalmii kalmii*
—White discal maculae of hemelytral membrane indistinct and irregular in outline; eastern half of North America ..... *kalmii angustomarginatus*
19. Pale mark on vertex small, round; length 8-10mm ..... *peruvianus*
—Pale mark on vertex longitudinally elongate; length 11-15mm ..... *reclivatus reclivatus*

Melacoryphus A. Slater
(Fig. 12)

Melacoryphus A. Slater, 1988: 309. Type species: *Lygaeus lateralis* Dallas, 1852, original designation.

Included species: *Melacoryphus admirabilis* (Uhler), 1872 (*Lygaeus*); *Melacoryphus circumlitus* (Stål), 1862 (*Lygaeus*); *Melacoryphus facetus* (Say), 1831 (*Lygaeus*); *Melacoryphus lateralis* (Dallas), 1852 (*Lygaeus*); *Melacoryphus micropterus* A. Slater, 1988; *Melacoryphus nigrinervis* (Stål), 1874 (*Melanocoryphus*); *Melacoryphus pedregalensis* (Brailovsky), 1977b (*Neacoryphus*); *Melacoryphus rubicollis* (Uhler), 1894 (*Melanocoryphus*); *Melacoryphus rubriger* (Stål), 1862 (*Lygaeus*); *Melacoryphus rubrolimbatus* A. Slater, 1988.

BODY. Moderately robust; impunctate except immediately before and behind callus and on prosternum and thoracic pleura; hairs short, decumbent, very sparse dorsally, dense on abdominal venter. Length 5.0-9.0mm. *Head* (fig. 12a) moderately declivent; vertex convex; ocellus distinctly raised above surface mesally and posteriorly, distance between ocelli about seven times distance from ocellus to eye; buccula moderately produced, ventral margin moderately convex. *Pronotum* with posterior width about twice anterior width; medial length slightly greater than anterior width; anterior margin concave, raised, not beaded, separated from callus by deeply punctate depression; posterior margin slightly convex laterally, slightly concave medially; lateral margins slightly convex posteriorly, slightly concave anteriorly; callus distinct, callar impressions unbranched, sinuate; impression just posterior to callus shallow, deeply punctate, extending over about anterior third of posterior lobe, interrupted medially by distinct carina, punctures becoming shallower posteriorly. *Scutellum* with length about 0.9 times width; stem and arms of median carina broad; lateral fovea distinct posteriorly, bottom smooth. *Hemelytron* slightly surpassing apex

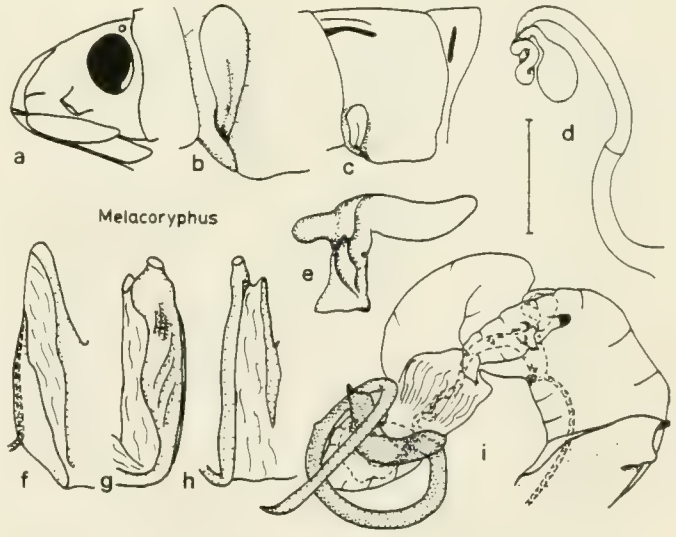


Fig. 12. a-h. *Melacoryphus lateralis* (Dallas). a. Head. b. Ostiolar peritreme and evaporative area. c. Metapleuron. d. Spermatheca. e. Left clasper, right lateral view. f-h. Ovipositor, left valvula and connecting membrane: f, first valve, ventral view; g, second valve, lateral view; h, second valve, ventral view. i. *Melacoryphus rubriger* (Stål), partially inflated aedeagus, left lateral view. Scale (mm): a,c = 1.0; b,d,f-h = 0.5; e,i = 0.375.

of abdomen; corial veins distinct, strongly raised; membrane opaque. *Propleuron* divided into three parts by dorsoventral impressions, anterior and posterior parts strongly punctate, median part convex. *Mesopleuron* divided into anterior and posterior sections by dorsoventral impression, posterior part moderately punctate. *Metapleuron* (fig. 12c) with shallow punctures or striae posteriorly; posterior margin directed dorsoventrally, convex, posterior margin of acetabula not produced posteriorly; ostiolar peritreme (fig. 12b) with anterior margin of channel higher than posterior margin, apical button narrowly ovate with long axis dorsoventrally directed, distinctly separated from surrounding pleuron dorsally and posteriorly; evaporative area moderately large, not surrounding dorsal part of peritreme but distinct before and behind it. *Abdomen* without anterolateral scars; sternum II fully exposed; sternum VI of female about half as long medially as laterally; sternum VII of female cleft to base. *GENITALIA.* — *Clasper* (fig. 12e) with blade almost at right angle to shank, strongly curved, flattened horizontally; posterior projection thumblike, well developed; shank with rooflike interior projection near junction with blade, two longitudinal ridges basad of projection separated by a distinct groove, a short anterior ridge near junction with blade. *Aedeagus* (fig. 12i) bent before telescoping into phallotheca; conjunctiva with well-developed lateral lobes near apex bearing series of small sclerotized spines; vesica strongly, asymmetrically swollen proximad of ring sclerite but without lobes or spines either proximad or distad of ring sclerite; ring sclerite well developed, with bluntly pointed apical extension; gonoporal process moderately elongate, robust; apical process of secondary gonopore short, acute; phallotheca without apical flange, process projecting, broad, scoop-shaped. *Spermatheca* (fig. 12d) with basal tube of moderate length, thick, without swelling; apical tube moderately elongate, pigmented, about as thick as basal tube basally, becoming coiled and slightly thinner than basal tube just basad of apical bulb, apical bulb distinct, somewhat irregular in outline, usually narrow but sometimes broad, apex usually blunt but sometimes acute. *Ovipositor* moderately elongate; first valve (fig. 12f) with connecting membrane cleft to about half distance to base and with long apical projection to either side of cleft, Y-sclerite distinct, reaching around apex of membrane; second valve (figs. 12g,h) with connecting membrane cleft to about one-third distance from base and with secondary cleft laterad of median cleft, resulting in short apical projection at apex of median cleft, distinct sclerite along lateral margin of median cleft and extending about half distance from base of cleft to base of membrane, valvula flattened with series of oblique grooves and ridges at middle and longitudinal grooves and ridges subapically. *COLOR.* — *Head* black. *Pronotum* black except usually humeral angles, anterior margin, and a median line on the posterior lobe red or orange. *Scutellum* black, often with red or orange apex. *Hemelytron* with clavus brown or black, scutellar margin sometimes red or orange; corium brown or black, costal margin usually and apical margin sometimes red or orange; membrane dark brown to black with apical margin and sometimes basal margin white. *Thoracic pleura* usually dark except narrow pale yellow acetabular and posterior margins. *Abdomen* ventrally brown or black, lateral margins sometimes red or orange.

DISTRIBUTION. Most species are Nearctic in distribution with only two species reaching southern Mexico and a single species reaching northern South America. One species is endemic to Guadalupe Island (Mexico). The exact range of most species is uncertain due to confusion between species in the older literature.

COMMENTS. The combination of raised hemelytral veins, flattened and coarsely punctate posterior pronotal lobe, very sparse dorsal pubescence, and lack of yellow in the color pattern characterizes members of *Melacoryphus*. In overall appearance its members perhaps most resemble species of *Dalmochrimnus*, which may be easily distinguished by their dense dorsal pubescence. *Melacoryphus* species are difficult to separate from those belonging to *Neacoryphus* on the basis of individual characters, but the overall appearance of members of the two genera is quite different. As mentioned under *Lygaeospilus*, that genus may simply be composed of very small species of *Melacoryphus*. I have followed a conservative course in recognizing both genera here since there do appear to be consistent differences between the two groups.

KEY TO SPECIES OF *MELACORYPHUS* A. SLATER (A. SLATER, 1988)

1. Micropterous, wings not or just reaching abdominal tergum II ..... *micropterus*
—Macropterous or submacropterous, wings reaching or nearly reaching apex of abdomen 2
2. Basal margin of hemelytral membrane white 3
—Basal margin of hemelytral membrane dark brown or black 5
3. Hemelytral membrane translucent white with contrasting brown markings along veins ..... *nigrinervis*
—Hemelytral membrane brown to black with only margins white 4
4. Dark markings of clavus and corium black; frequently with apical third of corium and half of clavus nearest scutellum red ..... *admirabilis*
—Dark markings of hemelytra light brown; irregular apical border of corium and narrow scutellar border of clavus red ..... *pedregalensis*
5. Clavus and corium completely dark brown to black ..... *rubicollis*
—At least costal margin of corium red or orange 6
6. Apical margin of corium red ..... *circumlitus*
—Apical margin of corium dark brown to black 7
7. Abdomen with distinct, sharply defined red lateral margins 8
—Abdomen nearly unicolored, without contrasting lateral margins 9
8. Light markings orange; scutellar and commissural margins of clavus narrowly but distinctly orange ..... *facetus*
—Light markings red; scutellar and commissural margins of clavus at most reddish ..... *rubrolimbatus*
9. Scutellum black; coloration bright; red costal margin of corium narrowed only slightly in apical third; usually an indistinct subbasal white macula on hemelytral membrane ..... *lateralis*
—Apex of scutellum red; coloration dull; red costal margin of corium strongly narrowed in apical third; no white macula on hemelytral membrane ..... *rubriger*

Melanopleurus Stål
(Fig. 13)

Lygaeus (*Melanopleurus*) Stål, 1874: 105, 109. Type species: *Lygaeus bicolor* Herrich-Schäffer, 1850, designated by Van Duzee, 1916. *Melanopleurus* Slater, 1964a: 146.

Kalinckacoris Brailovsky, 1978a: 116-117. Type species: *Kalinckacoris matucanae* Brailovsky, 1978, monobasic. **n. syn.**

Included species: *Melanopleurus amnigena* (Brailovsky & Barrera), 1984 (*Kalinckacoris*), **n. comb.**; *Melanopleurus aureus* (Distant), 1882 (*Lygaeus*), **n. comb.**; *Melanopleurus barrerai* Brailovsky, 1979a; *Melanopleurus belfragei* (Stål), 1874 (*Lygaeus* (*Melanopleurus*)); *Melanopleurus bicolor* (Herrich-Schäffer), 1850 (*Lygaeus*) = *Lygaeus bipartitus* Signoret, 1860, fide Stål, 1874 = *Lygaeus dimidiatus* Walker, 1872, preocc. fide Distant, 1882; *Melanopleurus bistriangularis* (Say), 1831 (*Lygaeus*); *Melanopleurus bistriangularis marginellus* (Dallas), 1852, (*Lygaeus*); *Melanopleurus brevis* Brailovsky, 1975; *Melanopleurus complicatus* Brailovsky, 1975; *Melanopleurus fuscosus* Brailovsky, 1977d; *Melanopleurus inflatus* Brailovsky, 1979a; *Melanopleurus maculicorium* Maldonado-Capriles, 1974; *Melanopleurus matucanae* (Brailovsky), 1978a (*Kalinckacoris*), **n. comb.**; *Melanopleurus nubilis* Brailovsky, 1979a; *Melanopleurus perplexus* Scudder, 1981; *Melanopleurus pyrrhopterus* (Stål), 1874 (*Lygaeus* (*Ochrostomus*)); *Melanopleurus pyrrhopterus melanopleurus* (Uhler), 1893 (*Lygaeus*); *Melanopleurus tener* Brailovsky, 1979a; *Melanopleurus tetraspilus* (Stål), 1874 (*Lygaeus* (*Melanopleurus*)); *Melanopleurus vazquezae* Brailovsky, 1979a; *Melanopleurus villai* Brailovsky, 1979a.

BODY. Robust; impunctate except pronotum immediately before and behind callus, and on prosternum; hairs short, dense, decumbent, sometimes interspersed with longer upright hairs. Length 4.0-10.0mm. *Head* (fig. 13a) strongly declivent; vertex convex; ocellus slightly raised above surface, distance between ocelli about five times distance from ocellus to eye; buccula moderately to strongly produced, ventral margin moderately to strongly convex. *Pronotum* with posterior width slightly less than twice anterior width; medial length about equal to anterior width; anterior margin concave, slightly raised but not beaded, separated from callus by shallow depression with shallow, sparse punctation; posterior margin slightly convex; lateral margins almost straight; callus indistinct, callar impressions unbranched or with vestigial branch, curving evenly toward anterior angles; impression just posterior to callus shallow, with sparse, shallow punctation, interrupted medially by low carina. *Scutellum* with length about 0.7 times width; stem and arms of median carina broad; lateral fovea distinct anteriorly, obsolete posteriorly, bottom smooth. *Hemelytron* slightly surpassing apex of abdomen; corial veins distinct, slightly raised; membrane opaque. *Propleuron* impunctate, almost flat except acetabula convex. *Mesopleuron* impunctate, almost flat except acetabula convex. *Metapleuron* (fig. 13c) impunctate; posterior margin angled slightly anterodorsad, posterior margin of acetabula not produced posteriorly; ostiolar peritreme (fig. 13b) with anterior margin of channel higher than posterior margin, apical button rounded, distinct from surrounding pleuron dorsally and posteriorly; evaporative area small, surrounding dorsal part of peritreme. *Abdomen* without anterolateral scars; sternum II fully exposed; sternum VI of female about three-fifths as long medially as laterally; sternum VII of female cleft to base. *GENITALIA.* — *Clasper* (fig. 13h) with blade at right angle to shank, moderately curved, somewhat dorsoventrally flattened and twisted so that flat side is somewhat ventrally directed, ventral margin slightly rugose; posterior projection moderately to strongly produced, conical or subconical; shank without rooflike interior projection, posterior ridge about evenly developed throughout, median ridge apparently absent, a small tooth anteriorly below juncture with blade. *Aedeagus* (fig. 13i) bent before telescoping into phallotheca; conjunctiva elongate, sharply bent ventrally, with lateral lobes near middle well developed, blunt, somewhat dorsally directed, bearing a dense field of small spines apically; vesica proximad of ring sclerite short, with one very elongate lobe bearing a single apical spine and a shorter lobe with an apical spine and, arising from it, two sublobes each armed with a single spine at the apex, vesica distad of ring sclerite without lobes or projections; ring sclerite very narrow, strongly sclerotized; gonoporal process short, slender; apical process of secondary gonopore short, acute. *Spermatheca* (fig. 13d) with basal tube elongate, without swelling; apical tube shorter than basal tube, about as thick as basal tube, coiled apically; apical bulb elongate, complexly coiled, not differentiated from adjacent tube. *Ovipositor* moderately elongate; first valve (fig. 13e) with connecting membrane extending beyond apex of valvifer by about one-third length of valvifer, cleft to about level with apex of valvula, Y-sclerite well developed basally, extending around apex of membrane; second valve (figs. 13f,g) with connecting membrane cleft almost to base, with short, acute projection at side of cleft, with distinct Y-sclerite reaching almost to apex of cleft, valvula swollen along ventral margin, flat subapically, slightly convex apically. *COLOR.* — *Head* black except buccula and small spot on vertex pale. *Pronotum* black except sometimes humeri reddish orange. *Scutellum* black. *Hemelytron* usually bright orange red, occasionally with infuscate area on corium or completely dark brown except basal angle; membrane dark brown usually with narrow white apical margin. *Thoracic pleura* black. *Abdomen* ventrally orange red except segment VII and genital segments black, sometimes lateral margins of some or all segments black.

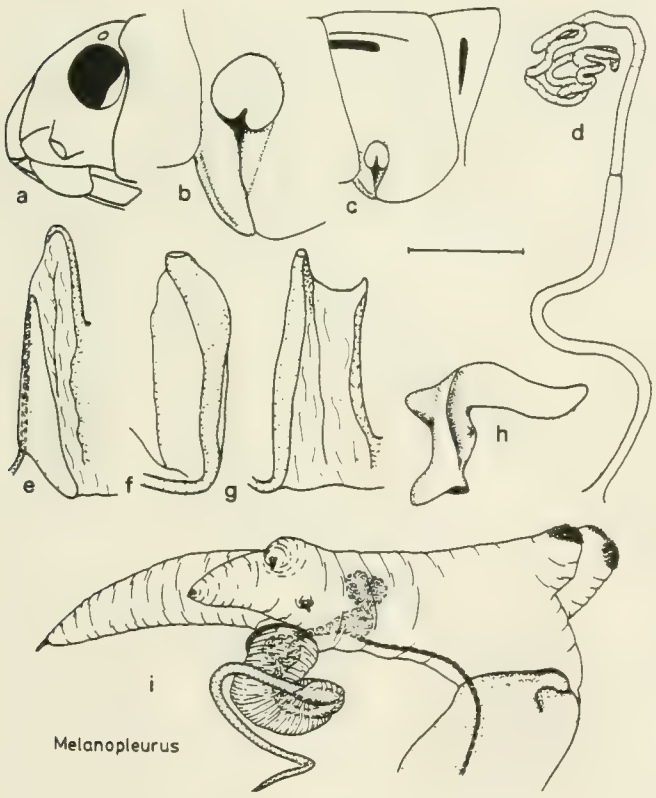


Fig. 13. a-h. *Melanopleurus bicolor* (Herrich-Schäffer). a. Head. b. Ostiolar peritreme and evaporative area. c. Metapleuron. d. Spermatheca. e-g. Ovipositor, left valvula and connecting membrane: e, first valve, ventral view; f, second valve, lateral view; g, second valve, ventral view. h. Left clasper, right lateral view. i. *Melanopleurus belfragei* (Stål), partially inflated aedeagus, left lateral view (after P. D. Ashlock, unpublished drawing). Scale (mm): a,c = 1.0; b,d-g,i = 0.5; h = 0.375.

DISTRIBUTION. There is a high degree of endemism in this genus. Of the 19 recognized species two, both originally described in *Kalinckacoris*, are endemic to Peru, one is endemic to Cuba, one is endemic to the Dominican Republic, one is restricted to south central Canada, one is known only from Colorado, one occurs only on Santa Catalina Island and the adjacent mainland, one occurs only in southern Arizona, and five are restricted to south-central Mexico. Of the remaining six species one (possibly two) occurs from central Mexico to northern South America and the others

are broadly distributed from the southwestern United States to southern Mexico or Guatemala.

COMMENTS. Species of Brailovsky's genus *Kalinckacoris* were separated from those belonging to *Melanopleurus* primarily on the basis of their dark coloration. As I could find no significant differences between members of the two genera in either genitalia or external structure, I have synonymized the genera here. The structure of the aedeagus is unique among Lygaeinae. The lobes appearing near the middle of the conjunctiva are similar in appearance to, and may be homologous with, the subapical conjunctival lobes of other Lygaeinae, their apparent position being due to elongation of the apical part of the conjunctiva. This elongated part of the conjunctiva appears to take the place of that part of the vesica proximal to the ring sclerite, which is much shortened despite bearing elongate lobes. Another possibility is that the spine bearing lobes, treated here as vesical, are homologous with the subapical conjunctival lobes of other Lygaeinae. In that case, the median conjunctival lobes of *Melanopleurus* species are unique structures within the Lygaeinae.

KEY TO SPECIES OF *MELANOPLEURUS* STÅL

1. Hemelytra not extending beyond abdominal segment VII (brachypterous or submacropterous) 2
—Hemelytra extending beyond the apex of the abdomen (macropterous) 6
2. Abdominal sterna heavily infuscated, not contrastingly marked with red or orange and black ..... *perplexus*
—Abdominal sterna contrastingly marked with red or orange and black 3
3. Lateral margins of abdominal sterna IV-VI red or orange 4
—Lateral margins of abdominal sternite IV-VI black 5
4. Hemelytral membrane reaching base of abdominal segment VII; rostrum surpassing metacoxa ..... *brevis*
—Hemelytral membrane reaching base of abdominal segment VI; rostrum reaching metacoxa ..... *nubilis*
5. Lateral margins of abdominal sterna II and III black, black margins of sterna IV-VI broad ..... *tener*
—Lateral margins of abdominal sterna II and III orange, black margins of sterna IV-VI narrow ..... *villai*
6. White apical margin of hemelytral membrane very broad, especially laterally; ostiolar peritreme yellow 7
—White apical margin of hemelytral membrane, if present, narrow and about equally wide apically and laterally; ostiolar peritreme usually black or infuscated 8
7. Clavus and corium reddish ..... *pyrrhopterus pyrrhopterus*
—Clavus and corium grayish ..... *pyrrhopterus melanopleurus*
8. Clavus and corium dark brown to black with at most base of clavus and narrow costal margin of corium orange 9
—Clavus and corium orange or red, sometimes with contrasting black maculae 10
9. Lateral pronotal margins orange ..... *amnigena*
—Pronotum entirely black ..... *matucanae*
10. Pronotum dark reddish brown ..... *aureus*
—Pronotum black except occasionally humeral angle orange 11
11. Ostiolar peritreme yellow ..... *complicatus*
—Ostiolar peritreme black 12
12. Corium red or orange with black markings 13
—Corium uniformly red or orange 15
13. Clavus with a central black mark ..... *tetraspilus*
—Clavus without black markings 14
14. Black corial macula touching costal margin at about middle ..... *maculicorium*
—Black corial marking discal, not touching costal margin ..... *fuscosus*
15. Hemelytral membrane uniformly dark brown, without white apical margin ..... *inflatus*
—Hemelytral membrane with white apical margin 16
16. Bucculae greatly expanded, very strongly convex anteriorly, truncate or angulate posteriorly; length at least 8mm 17
—Bucculae at most moderately expanded, evenly convex; length at most 6mm 18
17. Buccula truncate posteriorly; clavus and corium bright red ..... *belfragei*
—Buccula angulate posteriorly; clavus and corium orange-red ..... *bicolor*
18. Humeral angle of pronotum orange 19
—Pronotum entirely black or with at most posterior margin of humeral angle orange 20
19. Lateral margins of abdominal sterna orange; rostrum reaching mesocoxa ..... *bistriangularis bistriangularis*
—Lateral margins of abdominal sterna black; rostrum reaching metacoxa ..... *barrerai*
20. Lateral margins of abdominal sterna IV-VI orange 21
—Lateral margins of abdominal sterna IV-VI black ..... *villai*
21. Pronotum, hemelytra, and abdominal sterna with dense, coarse pubescence; rostrum surpassing apex of metacoxa ..... *vazquezae*
—Pronotum, hemelytra, and abdominal sterna with sparse, delicate pubescence; rostrum reaching apex of mesocoxa ..... *bistriangularis marginellus*

Neacoryphus Scudder
(Fig. 14)

Neacoryphus Scudder, 1965: 34. Type species: *Lygaeus bicrucis* Say, 1825, original designation.

Included species: *Neacoryphus bicrucis* (Say), 1825 (*Lygaeus*); *Neacoryphus verecundus* (Distant), 1882 (*Lygaeus* (*Ochrostomus*)), **n. comb.**

Incertae sedis species: *Neacoryphus albonotatus* (Barber), 1923 (*Lygaeus* (*Melanocoryphus*)); *Neacoryphus circumlinitus* (Distant), 1882 (*Lygaeus* (*Melanocoryphus*)); *Neacoryphus rubrocephala* Brailovsky, 1977b.

BODY. Robust; impunctate except most of pronotum and on prosternum and pro- and mesopleura; hairs short, decumbent, very sparse dorsally, denser on abdominal venter. Length 7.0-9.0mm. *Head* (fig. 14a) moderately declivent; vertex convex; ocellus distinctly raised above surface mesally and posteriorly, distance between ocelli about seven times distance from ocellus to eye; buccula moderately produced, ventral margin moderately convex. *Pronotum* with posterior width slightly less than twice anterior width; medial length slightly greater than anterior width; anterior margin concave, not raised, separated from callus by punctate area, punctures deeper and coarser near callus; posterior margin slightly sinuate; lateral margins almost straight, slightly convex posteriorly; callus distinct, callar impressions unbranched, transverse medially, curving toward anterior angles laterally; shallow impression behind callus extending over about anterior half of posterior lobe, deeply punctate just behind callus, punctures becoming less dense and deep posteriorly, interrupted medially by distinct carina. *Scutellum* with length about 0.8 times width; stem and arms of median carina broad; lateral fovea distinct posteriorly, bottom smooth. *Hemelytron* surpassing apex of abdomen; corial veins distinct, strongly raised. *Propleuron* divided into three parts by dorsoventral impressions, anterior and posterior parts almost flat and strongly punctate, median part slightly convex and impunctate. *Mesopleuron* divided into anterior and posterior sections by dorsoventral impression, posterior part punctate. *Metapleuron* (fig. 14c) impunctate; posterior margin directed dorsoventrally, convex, posterior margin of acetabula not produced posteriorly; ostiolar peritreme (fig. 14b) with anterior margin of channel higher than posterior margin, apical button rounded, distinctly separated from surrounding pleuron dorsally and posteriorly; evaporative area small, surrounding dorsal part of peritreme. *Abdomen* without anterolateral scars; sternum II fully exposed; sternum VI of female about two-thirds as long medially as laterally; sternum VII of female cleft to base. *GENITALIA.* — *Clasper* (fig. 14h) with blade at slightly oblique angle to shank, moderately curved, somewhat dorsoventrally flattened, posterior projection conical, moderately developed, shank without rooflike interior projection, single longitudinal ridge on inner face projecting most strongly just below level of posterior projection, distinct groove just anterior to ridge, lower margin of blade with acute projection near base. *Aedeagus* (fig. 14i) bent before telescoping into phallotheca; conjunctiva short, without dorsal or subapical lateral lobes; vesica strongly, asymmetrically produced to form a transverse lobe projecting to either side proximad of ring sclerite, without projections distad of ring sclerite; ring sclerite well developed, without projections; apical process of secondary gonopore elongate, acute; phallotheca with flange along dorsal half of apical margin, process short, not distinct from flange. *Spermatheca* (fig. 14d) with basal tube thick, of moderate length, without swelling; apical tube thick, unpigmented except for thinner complexly coiled, heavily pigmented section just basad of apical bulb; apical bulb elongate, narrow, only slightly thicker than adjacent tube. *Ovipositor* moderately elongate; first valve (fig. 14e) with connecting membrane extending beyond apex of valvula about one-third valvular length, cleft medially to about half distance to base, strongly pigmented area extending from apex to just below level of cleft between cleft and valvula but not connected with either, Y-sclerite indistinct, scarcely extending above base of cleft; second valve (figs. 14f,g) with connecting membrane cleft medially to about half distance to base, with small apical projection at each side of cleft, valvula subapically swollen longitudinally along ventral margin, flattened along dorsal margin. *COLOR.* — *Head* black except buccula pale yellow, vertex lacking pale spot. *Hemelytron* with membrane dark brown with narrow white apical margin. The two included species are otherwise differently colored.

DISTRIBUTION. Neacoryphus bicrucis occurs from southern Canada to southern Brazil while *N. verecundus* is restricted to southern Mexico and Guatemala.

COMMENTS. The two species now placed in *Neacoryphus* differ so much in color pattern as to appear totally dissimilar externally. However, their genitalic and external structures are similar.

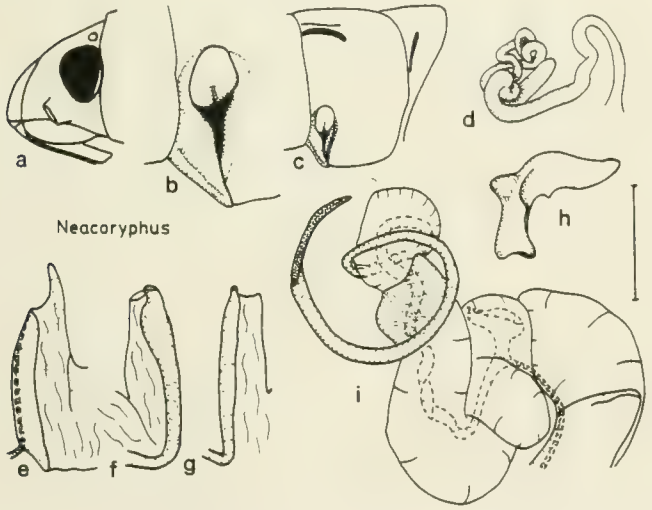


Fig. 14. *Neacoryphus bicrucis* (Say). a. Head. b. Ostiolar peritreme and evaporative area. c. Metapleuron. d. Spermatheca. e-g. Ovipositor, left valvula and connecting membrane: e, first valve, ventral view; f, second valve, lateral view; g, second valve, ventral view. h. Left clasper, right lateral view. i. Aedeagus, left lateral view. Scale (mm): a,c = 1.0; b,d-g,i = 0.5; h = 0.375.

KEY TO SPECIES OF *NEACORYPHUS* SCUDDER

1. Head dorsally black; corium bright or dull orange, veins concolorous with or paler than surrounding areas ..... *bicrucis*
—Head dorsally mostly ocher; corium ocher with veins contrasting dark brown ..... *verecundus*

Nicuesa Distant
(Fig. 15)

Nicuesa Distant, 1893: 385. Type species: *Nicuesa speciosa* Distant, 1893, monobasic.

Included species: *Nicuesa affinis* Distant, 1901; *Nicuesa speciosa* Distant, 1893; *Nicuesa oculata* Brailovsky & Brailovsky, 1979.

BODY. Slender, parallel sided, completely impunctate; hairs moderately dense, short, decumbent, longest on abdominal venter, interspersed long upright hairs on metasternum and mesal parts of abdominal sterna III and IV. Length 5.0-7.0mm. *Head* (fig. 15a) strongly declivent, vertex almost flat; eye carried on short stalk, stalk directed slightly dorsad; ocellus on a raised "bump," directed slightly laterad, distance between ocelli about 1.25 times distance from ocellus to eye; distinct lambda-shaped sulcus in front of ocellus reaching antenniferous tubercle; buccula scarcely produced, ventral margin straight. *Pronotum* with posterior width about 1.5 times anterior width; medial length about half poste-

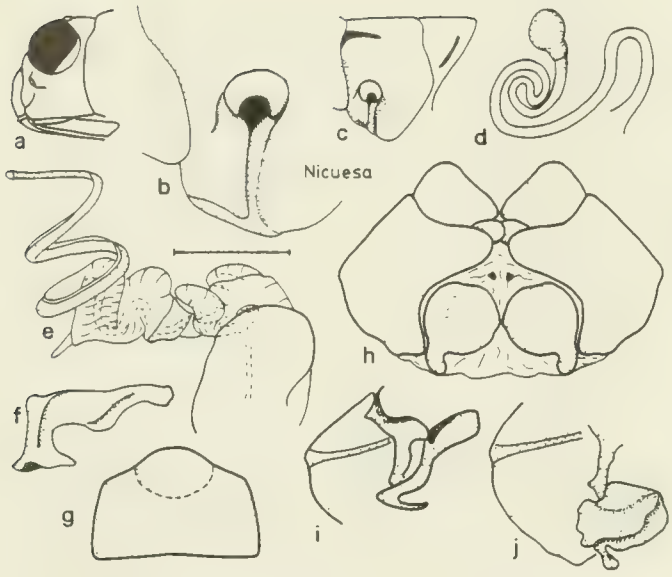


Fig. 15. *Nicuesa speciosa* Distant. a. Head. b. Ostiolar peritreme and evaporative area. c. Metapleuron. d. Spermatheca. e. Partially inflated aedeagus, left lateral view. f. Left clasper, right lateral view. g. Sternite VII, dorsal view. h-j. Ovipositor: h, ventral view; i, gonangulum and second valvifer, dorsal view; j, gonangulum and first valve, dorsal view. Scale (mm): a,c,g = 1.0; b,d = 0.5; e,f,h-j = 0.375.

rior width; anterior margin concave, raised; posterior margin slightly produced posteriorly laterad of scutellum; lateral margins slightly indented about one-third distance from anterior to humeral angles; callus not distinct, callar impressions unbranched, weakly sinuate, widely separated medially; disk of posterior lobe with M-shaped carina, most distinct laterally, and with anterolateral extension almost reaching anterior pronotal angle. *Scutellum* with length about 0.8 times width; median carina Y-shaped, stem about half as long as arms; lateral fovea distinct, bottom smooth. *Hemelytron* greatly surpassing apex of abdomen; corial veins indistinct; membrane opaque. *Propleuron* except dorsoventral median ridge depressed, depression accentuating bead of anterior margin behind eye. *Mesopleuron* except dorsoventral median ridge depressed. *Metapleuron* (fig. 15c) depressed medially; posterior margin directed anterodorsally, concave just ventrad of posterolateral angle, otherwise convex, posterior margin of acetabula not produced, occupying about half posterior margin of pleuron; ostiolar peritreme (fig. 15b) stalked, projecting dorsolaterally, anterior margin of channel not higher than posterior margin, apical button oblong with long axis directed anteroposteriorly; evaporative area broad, covering about one-sixth area of pleuron, extending onto posterior margin of mesopleuron. *Abdomen* without anterolateral scars; sternum II fully exposed; sternum VI of female about as long medially as laterally; sternum VII of female (fig. 15g) not cleft, produced posteriorly to hide ovipositor from below. *GENITALIA.* — *Clasper* (fig. 15f) with blade at right angle to shank, flattened dorsoventrally, straight except sharply curved inward at tip, a swollen oblique ridge ventrally near middle, shank much shorter than blade, without rooflike interior projection, a sharp longitudinal ridge from near base to base of blade on interior surface, posterior projection reduced to lump. *Aedeagus* (fig. 15e) telescoping directly into phallotheca; conjunctiva attached at about two-thirds distance from base to apex of phallotheca, small lobe on each side near apex of phallotheca, without spines; vesica with tubular basal lobe on right side, striate and with thin conical projection apically; ring sclerite well developed, cup-shaped; gonoporal process coiled, with membranous flange almost to apex; secondary gonopore slightly expanded, without process; phallothecal projection a large, moderately convex, dorsally directed flange with a medially directed flange on its mesal face. *Spermatheca* (fig. 15d) with basal tube long, moderately thick, without swelling; apical tube absent; pigmented apical bulb pear-shaped, without flanges. *Ovipositor* (figs. 15h-j) highly modified, flattened, platelike, lacking rami, apex of gonangulum free; first valvifer produced mesally, almost completely covering second valvifer; first valvula short, almost circular in outline, with large flange on inner surface; second valvifer elongate, produced mesally to meet when valve closed; second valvula reduced to small sclerite completely surrounded by membrane. *COLOR.* — *Head* black. *Pronotum* yellow or orange with or without median black line. *Scutellum* dark brown to black. *Hemelytron* dark brown to black except sometimes narrow yellow costal margin; membrane dark brown to black with narrow pale apical margin. *Thoracic pleura* dark brown to black except propleuron usually pale yellow or orange. *Abdomen* ventrally dark brown to black.

DISTRIBUTION. Nicuesa species are known only from Panama and northwestern South America. The species *N. oculata* is known from a single collection from Peru. There is some doubt as to the distinctness of the other two species, as *N. affinis*, known only from the type locality in Ecuador, may be merely a color variant of *N. speciosa*, which is known from Panama and Venezuela.

COMMENTS. Species belonging to *Nicuesa* have the most highly modified female genitalia of any Lygaeinae. The platelike ovipositor, which is completely covered by the extended abdominal sternum VII, approaches the pentatomoid ovipositor in general appearance. However, the two types of ovipositor cannot be considered homologous because the development of the various sclerites involved is entirely different. The reduction of the second valvula to a tiny sclerite completely surrounded by membrane is reminiscent of the condition in some Rhopalidae. The free apex of the gonangulum may be unique among Pentatomomorpha. In contrast to the extreme modification of the ovipositor, the aedeagus shows remarkably little modification. The greatly expanded conjunctival or vesical lobes found in other pentatomomorphs with reduced ovipositors are missing. The claspers, however, are greatly enlarged and modified. It may be that they play a greater role in maintaining connection during copulation than is the case with other pentatomomorphs.

KEY TO SPECIES OF *NICUESA* DISTANT

1. Pronotum with a broad longitudinal median brown line ..... *oculata*
—Pronotum completely red or yellow 2
2. Pronotum yellow ..... *affinis*
—Pronotum red ..... *speciosa*

***Ochrimnus* Stål**
(Figs. 16-20)

Ochrimnus Stål, 1874: 114. Type species: *Lygaeus collaris* Fabricius, 1803, designated by Slater, 1964a.

Included species: See subgenera.

BODY. Slender to moderately robust; impunctate except occasionally on pronotum in front of callus; hairs short, fine, decumbent, sparse to moderately dense dorsally, denser on abdominal venter. Length 4.0-9.0mm. *Head* (figs. 16a, 17a, 18a, 19a, 20a) moderately to strongly declivent; vertex convex; ocellus distinctly raised above surface mesally and posteriorly; buccula occasionally very short, slightly to strongly produced, ventral margin moderately to strongly convex. *Pronotum* with anterior margin concave, raised at least laterally; posterior margin slightly sinuate or convex; lateral margins variable, usually straight or almost so; callus distinct, callar impressions transverse medially, curving toward anterior an-

gles laterally, with posterior branch at about one-third distance from mesal end, this extending onto lateral postcallar carina; postcallar impression impunctate, very distinct just behind callus, appearing as a transverse series of four dashes when viewed under low magnification due to interruption by distinct median and lateral carinae and to lack of extension onto posterior lobe. *Scutellum* with length from about 0.67 to 0.8 times width; stem and arms of median carina about equally broad; lateral fovea usually distinct posteriorly, bottom smooth. *Hemelytron* usually surpassing apex of abdomen, occasionally shorter; corial veins most distinct basally, slightly raised; membrane opaque. *Propleuron* divided into three parts by distinct dorsoventral impressions, impunctate, median part slightly convex. *Mesopleuron* divided into anterior and posterior sections by shallow dorsoventral impression, impunctate. *Metapleuron* (figs. 16c, 17c, 18c, 19c, 20c) impunctate; posterior margin directed dorsoventrally, posterior margin of acetabula produced posteriorly; ostiolar peritreme (figs. 16b, 17b, 18b, 19b, 20b) with anterior margin of channel higher than posterior margin, apical button rounded, distinctly separated from surrounding pleuron dorsally and posteriorly; evaporative area small, surrounding dorsal part of peritreme. *Abdomen* without anterolateral scars; sternum II fully exposed; sternum VI of female half to two-thirds as long medially as laterally; sternum VII of female cleft to base. *GENITALIA.* — *Clasper* (figs. 16h, 17e, 18h, 19j, 20f) with blade at about a right angle to shank, thin at least apically, moderately curved, somewhat laterally flattened, twisted so that inner face is somewhat ventrally directed; posterior projection at most represented by a distinct bulge; shank with inner face slightly concave, without distinct ridges, without rooflike interior projection but with an elongate variously shaped projection usually attached at junction with blade but occasionally at posterior edge. *Aedeagus* (figs. 16j, 17i, 18i, 19h,i, 20e) bent before telescoping into phallotheca; conjunctiva short, usually without lobes; vesica proximad of ring sclerite with varying number (usually two) basal lobes bearing spines, distad of ring sclerite usually with a single spine-bearing projection; ring sclerite obsolete; gonoporal process short, slender to moderately robust; secondary gonopore with short acute process; phallotheca usually without discal ridges, process variable. *Spermatheca* (figs. 16d, 17d, 18d, 19g, 20d) with basal tube short, slender, without swelling; apical tube long, slender, irregularly coiled just basad of apical bulb; apical bulb narrow, elongate, apex acute. *Ovipositor* short or elongate, usually slender; membrane with distinct basal pockets (fig. 16i); first valve (figs. 16e; 17f; 18e; 19d; 20g) with connecting membrane cleft medially, extending at least slightly beyond apex of valvula, often pigmented or lightly sclerotized, usually without Y-sclerite, valvifer triangular, valvula narrow, subtriangular, ramus not reaching apex; second valve (figs. 16f,g; 17g,h; 18f,g; 19e,f; 20h,i) with connecting membrane pigmented or lightly sclerotized, cleft medially, a shoulder or small apical projection at each side of cleft. *COLOR.* — Variable, usually predominantly drab ochers and browns, occasionally with contrasting orange markings, especially on pronotum.

DISTRIBUTION. The genus as a whole ranges from the southern United States south to central Argentina. There is considerable overlap in the distributions of the subgenera.

COMMENTS. The presence of a series of four lateral dash-like impressions behind the callus is diagnostic for *Ochrimnus*. Although the five subgenera recognized here are easily differentiated, I have chosen not to raise them to generic rank so as not to obscure the well-defined group to which they all belong. The assignment of individual species to subgenera is based primarily on the structure of the ovipositor and on external structure and coloration. It would have been preferable to use the distinctive development of the base of the vesica, but I was unable to obtain the necessary complete aedeagal inflations for many species.

KEY TO SUBGENERA AND SPECIES OF *OCHRIMNUS* STÅL

1. Abdominal sterna III-VI either red (sometimes with yellow posterior margins on some segments) or black with yellow posterior margins ..... *Ochrimnus* (*Aglaochrimnus*) 5
—Abdominal sterna III-VI if with red markings then either predominantly yellow with transverse red marks or variegated with red, yellow, and brown, never black with yellow posterior margins 2
2. Abdominal sternite VI of female about 1/3 as long medially as laterally; anterior pronotal lobe either completely orange or yellow or with margins pale yellow and disc orange, red, or brownish red, or if anterior lobe with extensive dark markings then entire pronotum brown except narrow longitudinal median line, not significantly broader posteriorly and narrow margins pale ..... *Ochrimnus* (*Phaeochrimnus*) 12
—Abdominal sternite VI of female about equally long medially and laterally; anterior pronotal lobe with extensive dark markings, usually connected with dark markings of posterior lobe, posterior lobe markings either separated by a longitudinal median line distinctly broader posteriorly than anteriorly or without median line, or if anterior lobe without dark markings then posterior lobe also without dark markings 3
3. Pronotum subquadrate, predominantly dark brown with pale markings yellow; base of corium and clavus pale; apical margin of corium completely pale and much broadest at apical angle ..... *Ochrimnus* (*Orthochrimnus*) 20
—Pronotum much narrower anteriorly than posteriorly, usually with extensive pale markings, pale markings often orange; base of corium and clavus dark; apical margin of corium if completely pale then about equally broad throughout 4
4. Robust; posterior lobe of pronotum usually predominantly orange or predominantly dark brown with orange lateral and posterior margins, if with extensive dark maculae on either side of midline then basal 2/3 of corium dark brown and apical 1/3 orange; disc of anterior pronotal lobe brown without pale median line ..... *Ochrimnus* (*Ochrimnus*) 23
—Slender; posterior lobe of pronotum pale yellow or orange with extensive dark macula on either side of midline or if without dark markings than anterior lobe also without dark markings; anterior lobe often with pale median longitudinal line; corium never brown basally and orange apically ..... *Ochrimnus* (*Parochrimnus*) 30
5. Abdominal sterna black with yellow posterior margins ..... *pallidocinctus*
—Abdominal sterna red, sometimes with pale yellow posterior margins 6
6. Pronotum with distinct yellow longitudinal median line ..... *conjunctus*
—Pronotum without longitudinal median line 7
7. Dark markings of pronotum, especially anterior lobe, and of corium reddish ..... *languidus*
—Dark markings of pronotum and corium black 8
8. Length less than 6.5mm; lateral pronotal margins black or very narrowly and indistinctly yellow ..... *disseptus*

—Length more than 7mm; lateral pronotal margins distinctly yellow, sometimes interrupted at middle or at humeral angles 9
9. Costal margin of corium pale orange, basal 1/3 less than half as wide as pale posterior margin ....*mirum*
—Costal margin of corium yellow, basal 1/3 at least half as wide as pale posterior margin 10
10. Pale lateral margins of pronotum interrupted at middle; black marking of pronotal disc not constricted just behind callus ....*lynceus*
—Pale lateral margins of pronotum complete or interrupted just in front of humeral angles: black marking of pronotal disc distinctly constricted just behind callus....11
11. Posterior margin of abdominal sternite VI yellow ....*schizus*
—Posterior margin of abdominal sternite VI red ....*cellus*
12. Anterior pronotal lobe either completely orange or yellow or with margins pale yellow and disc orange, red, or brownish red, if dark markings present then only a fuscous spot near anterior margin on either side of midline not approaching dark markings of posterior lobe 13
—Pronotum predominantly dark except pale margins and narrow longitudinal median line 17
13. Anterior pronotal lobe completely margined with pale yellow 14
—At least posterior margin of anterior pronotal lobe not margined with pale yellow 16
14. Antenniferous tubercles acutely produced laterad of antennal insertion....*gerulus*
—Antenniferous tubercles not acutely produced laterad of antennal insertion 15
15. Dorsum of head with a slightly curved longitudinal black mark to either side of midline just mesad of ocellus ....*limbatipennis*
—Dorsum of head without distinct longitudinal black marks at base....*pallescens*
16. Dorsum of head black; femora unicolored....*bellissimus*
—Dorsum of head yellow on either side of midline in front of eyes; femora brown with base and apex pale yellow ....*mimulus*
17. Bucculae strongly produced, ventral margin more strongly convex anteriorly than posteriorly....18
—Bucculae moderately produced, ventral margin about evenly convex throughout 19
18. Femora entirely brown....*rabidus*
—Femora brown basally, yellow apically....*interstinctus*
19. Apical margin of corium yellow, contrasting with brown discal coloration ....*luteolus*
—Apical margin of corium brown, concolorous with brown discal coloration....*dimorphopterus*
20. Hemelytra reduced, not covering connexiva V-VII 21
—Hemelytra not reduced, covering connexiva V-VII 22
21. Hemelytra not surpassing abdominal tergum V; pronotal pubescence dense ....*testatus*
—Hemelytra reaching abdominal tergum VII; pronotal pubescence sparse ....*nitidulus*
22. About basal 1/2 of clavus pale yellow; yellow costal margin of corium broadly interrupted just beyond middle ....*cinctipennis*
—Clavus black except commissural margin; yellow costal margin of corium entire or narrowly interrupted near apex ....*neotropicalis*
23. Antennal segment IV yellow except extreme base; dorsum black except indistinct ocher pronotal and corial margins....*nigriceps*
—Antennal segment IV dark brown to black; dorsum with distinct, usually extensive, orange and/or yellow markings 24
24. Corium dark brown to black except about apical 1/3 orange; posterior pronotal lobe orange with a large dark brown to black macula on either side of midline extending from callus to posterior margin ....*tripligatus*
—Corium dark brown to black with costal and apical margins and often veins pale yellow; posterior pronotal lobe variably colored but never with large distinct maculae on either side of midline reaching posterior margin 25
25. Posterior pronotal lobe entirely orange....26
—Posterior pronotal lobe with at least a short extension of dark marking of anterior lobe to either side of midline dark brown to black 27
26. Femora bicolored, basal 2/3 pale yellow, apical 1/3 light brown; veins of corium usually concolorous with surrounding areas ....*collaris*
—Femora unicolored, light brown; veins of corium always pale yellow, contrasting with dark brown surrounding areas ....*laevus*
27. Dark markings of posterior pronotal lobe restricted to a short fingerlike extension of dark markings of anterior lobe on either side of midline 28
—Dark markings of posterior pronotal lobe extensive, occupying almost entire disc 29
28. Abdominal sterna entirely black; length less than 7mm ....*marquezi*
—Abdominal sterna black medially, yellow or orange laterally; length more than 8mm ....*neothoracicus*
29. Femora bicolored, basal 2/3 pale yellow, apical 1/3 light brown; corial veins much lighter than surrounding areas....*pseudocollaris*
—Femora unicolored, light brown; corial veins only slightly lighter than surrounding areas ....*henryi*
30. Bucculae scarcely produced, extending posteriorly only about as far as anterior margin of eye....*cophinus*
—Bucculae moderately to strongly produced; extending posteriorly almost to base of head....31
31. Pronotum entirely red or orange ....*barberi*
—Pronotum with extensive dark markings....32
32. Disc of corium orange, occasionally with diffuse infuscation; corial veins never pale and contrasting with surrounding areas ....*foederatus*
—Disc of corium brown; corial veins often pale and contrasting with surrounding areas....33
33. Posterior pronotal lobe without distinct light markings, at most with posterior margin slightly lighter than disc, veins of hemelytral membrane darker than surrounding areas....*sceptrum*
—Posterior pronotal lobe with distinct light markings; veins of hemelytral membrane concolorous with surrounding areas....34

34. Pale markings of posterior pronotal lobe restricted to narrow lateral and broad posterior margins ..... *scalprum*
—Pale markings of posterior pronotal lobe extending onto disc as at least a median longitudinal line 35
35. Posterior pronotal lobe with a single dark longitudinal macula to either side of midline 36
—Posterior pronotal lobe with a large dark longitudinal macula to either side of midline and a smaller macula near or at each lateral margin 40
36. Hemelytral membrane with pale apical margin narrow and about equally wide throughout 37
—Hemelytral membrane with pale apical margin broad laterally and narrow apically 38
37. Pale pronotal markings yellowish; disc of posterior pronotal lobe predominantly dark ..... *sagax*
—Pale pronotal markings bright orange; disc of posterior pronotal lobe predominantly pale ..... *lineoloides*
38. Pale median longitudinal line of posterior pronotal lobe about twice as wide at posterior margin as just behind series of transverse impressions ..... *obsoletus*
—Pale median longitudinal line of posterior pronotal lobe at most as wide at posterior margin as just behind series of transverse impressions 39
39. Scutellum with raised lateral margins and most of longitudinal median carina yellow ..... *dallasi*
—Scutellum with only apex yellow ..... *carnosulus*
40. Hemelytral membrane with pale apical margin much broader laterally than apically ..... *succineus*
—Hemelytral membrane with pale apical margin narrow and about equally broad laterally and apically 41
41. Anterior pronotal margin without infuscated areas or these restricted to a small area to either side of midline; pale lateral margins of anterior pronotal lobe distinct ..... *chontalensis*
—Anterior pronotal margin almost completely infuscated; pale lateral margins of anterior pronotal lobe indistinct 42
42. Costal margin of corium distinctly yellow; yellow spot at vertex of head large ..... *somnus mulsus*
—Costal margin of corium pale, not distinctly yellow; yellow spot at vertex of head small ..... *somnus somnus*

Ochrimnus (Aglaochrimnus) new subgenus
(Fig. 16)

Type species: *Lygaeus pallidocinctus* Stål, 1862.

Included species: *Ochrimnus* (*Aglaochrimnus*) *cellus* Brailovsky, 1982a (*Ochrimnus*); *Ochrimnus* (*Aglaochrimnus*) *conjunctus* (Distant), 1882 (*Lygaeus* (*Ochrostomus*)); *Ochrimnus* (*Aglaochrimnus*) *disseptus* (Stål), 1874 (*Lygaeus* (*Ochrostomus*)); *Ochrimnus* (*Aglaochrimnus*) *languidus* Brailovsky, 1982a (*Ochrimnus*); *Ochrimnus* (*Aglaochrimnus*) *lynceus* Brailovsky, 1982a (*Ochrimnus*); *Ochrimnus* (*Aglaochrimnus*) *mirum* Brailovsky, 1982a (*Ochrimnus*); *Ochrimnus* (*Aglaochrimnus*) *pallidocinctus* (Stål), 1862 (*Lygaeus*); *Ochrimnus* (*Aglaochrimnus*) *schizus* Brailovsky, 1982a (*Ochrimnus*).

Structure as in generic description with the following additions. *BODY.* Moderately robust; impunctate; hairs short, fine, decumbent, fairly sparse dorsally, denser on abdominal venter. Length 6.0-9.0mm. *Head* (fig. 16a) moderately declivent; distance between ocelli about eight times distance from ocellus to eye; buccula moderately produced, ventral margin moderately convex. *Pronotum* with posterior width about 1.7 times anterior width; median length slightly greater than anterior width; anterior margin concave, raised, beaded laterally, separated from callus by narrow, indistinctly punctate, depressed area; posterior margin slightly sinuate; lateral margins almost straight. *Scutellum* with length about 0.75 times width; stem and arms of median carina about equally broad; lateral fovea distinct posteriorly, bottom smooth. *Hemelytron* surpassing apex of abdomen. *Metapleuron* (figs. 16b,c) with posterior margin directed dorsoventrally, convex. *Abdomen* with sternum VI of female about three-fifths as long medially as laterally. *GENITALIA.* — *Clasper* (fig. 16h) with blade about as long as shank, very broad basally, tapering rapidly to narrow apex; posterior projection represented by low, broad bulge; interior projection triangular, very broad basally, arising at juncture of shank and blade, line of attachment subparallel to blade. *Aedeagus* (fig. 16j) with conjunctiva short with small, unarmed, dorsally directed, subapical, lateral lobes; vesica basally with a bifid, unarmed lobe, and a single lobe bearing two stout, heavily sclerotized spines, the sclerotization extending over much of lobe and connecting bases of spines, strongly, asymmetrically swollen distad of basal lobes, and with a subapical lobe bearing an elongate spine with broadly sclerotized base; apical process of secondary gonopore short, acute; phallotheca concave laterally, dorsal margin not interrupted, distinct ridge along apical margin and one or more dis-

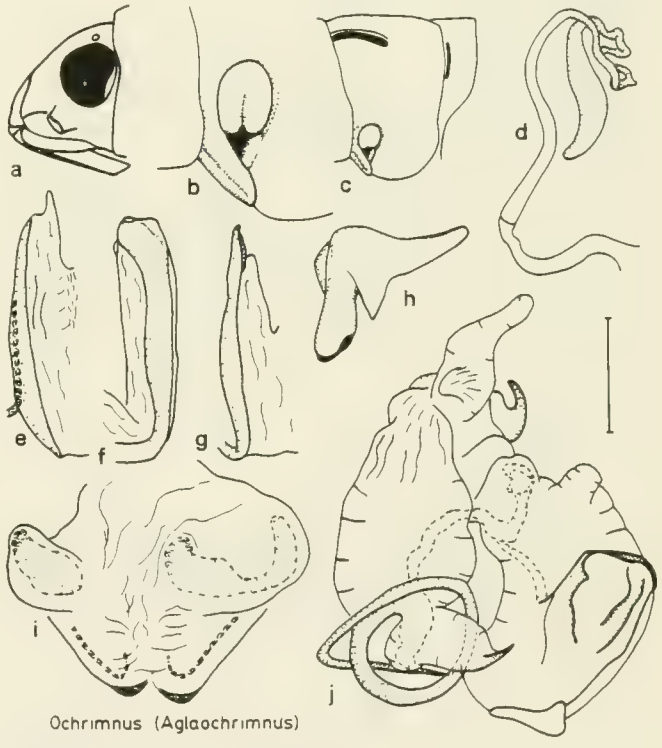


Fig. 16. a-h. *Ochrimnus* (*Aglaochrimnus*) *pallidocinctus* (Stål). a. Head. b. Ostiolar peritreme and evaporative area. c. Metapleuron. d. Spermatheca. e-g. Ovipositor, left valvula and connecting membrane: e, first valve, ventral view; f, second valve, lateral view; g, second valve, ventral view. h. Left clasper, right lateral view. i,j. *Ochrimnus* (*Aglaochrimnus*) *disseptus* (Stål). i. Ovipositor, basal pockets of membrane. j. Partially inflated aedeagus, left lateral view. Scale (mm): a,c = 1.0; b,d-g,i,j = 0.5; h = 0.375.

tinct longitudinal ridges on disc, without distinct process. *Spermatheca* (fig. 16d) with apical bulb much broader than adjacent tube. *Ovipositor* short, slender; first valve (fig. 16e) with connecting membrane extending slightly beyond apex of valvula as an acute projection, cleft to about two-thirds distance to base, pigmented laterad of cleft; second valve (figs. 16f,g) with connecting membrane cleft to about half distance to base, with small, blunt apical projection at each side of cleft, valvula slightly, evenly swollen along midline. *COLOR.* — *Head* dark brown to black except bucculae and rounded spot on vertex pale yellow or ocher. *Pronotum* dark brown to black, occasionally suffused with red, except anterior, posterior, and usually lateral margins pale yellow or orange. *Scutellum* dark brown to black with apex and sometimes raised lateral margins pale yellow. *Hemelytron* dark brown to black, occasionally suffused with red, except costal and apical margins of corium and claval commissure pale yellow or orange; membrane dark brown to black with very narrow apical and lateral margins white. *Thoracic pleura* predominantly dark brown to black with acetabular and posterior margins pale yellow. *Abdomen* dorsally red or brown; ventrally either predominantly red (sometimes with posterior margins of some segments narrowly yellow) except sternum VII and genital segments dark brown to black or transversely striped with dark brown and yellow.

DISTRIBUTION. Species of this subgenus occur from central Mexico to Bolivia. There is some, but not a great deal, of overlap in the distributions of individual species. Two species, *O.* (*A.*) *pallidocinctus* and *O.* (*A.*) *languidus*, have not been recorded south of Nicaragua. The other species are restricted to South America, with the exception of *O.* (*A.*) *disseptus* which occurs as far north as Panama. The South American species are all very similar in general appearance while the two northern species differ considerably both from each other and from the South American group.

COMMENTS. The name *Aglaochrimnus* is from the Greek and refers to the handsome overall appearance of members of the subgenus.

The large size, dark brown to black coloration with contrasting yellow margins, and flanges of the phallothecal disc separate species belonging to this subgenus from other *Ochrimnus* subgenera. All known species except *Ochrimnus* (*Aglaochrimnus*) *pallidocinctus* have red abdominal sterna. The structure of the clasper is very consistent among species. The sculpture of the phallotheca provides good specific characters.

Ochrimnus (Ochrimnus) Stål
(Fig. 17)

Ochrimnus Stål, 1874: 114. Type species: *Lygaeus collaris* Fabricius, 1803, designated by Slater, 1964a.

Included species: *Ochrimnus* (*Ochrimnus*) *collaris* (Fabricius), 1803 (*Lygaeus*); *Ochrimnus* (*Ochrimnus*) *henryi* Brailovsky, 1982a; *Ochrimnus* (*Ochrimnus*) *laevus* Brailovsky, 1982a; *Ochrimnus* (*Ochrimnus*) *marquezi* Brailovsky, 1982a; *Ochrimnus* (*Ochrimnus*) *neothoracicus* (Slater), 1964a (*Ochrostomus*) = *Lygaeus thoracicus* Stål, 1862, preocc. fide Slater, 1964a; *Ochrimnus* (*Ochrimnus*) *nigriceps* (Scudder), 1958 (*Ochrostomus*); *Ochrimnus* (*Ochrimnus*) *pseudocollaris* Brailovsky, 1982a; *Ochrimnus* (*Ochrimnus*) *tripligatus* (Barber), 1914 (*Lygaeus* (*Ochrostomus*)) = *Lygaeus* (*Ochrostomus*) *moa* Barber, 1947, fide Brailovsky, 1982a.

Structure as in generic description with the following additions. *BODY.* Moderately robust; hairs short, fine, decumbent, sparse dorsally, denser on abdominal venter. Length 5.5-9.0mm. *Head* (fig. 17a) moderately declivent; vertex slightly convex; distance between ocelli about 10 times distance from ocellus to eye; buccula moderately produced, ventral margin moderately convex. *Pronotum* with posterior width about 1.8 times anterior width; medial length and anterior width subequal; anterior margin raised, beaded laterally; posterior margin slightly convex; lateral margins straight or almost so. *Scutellum* with length about 0.66 times width;

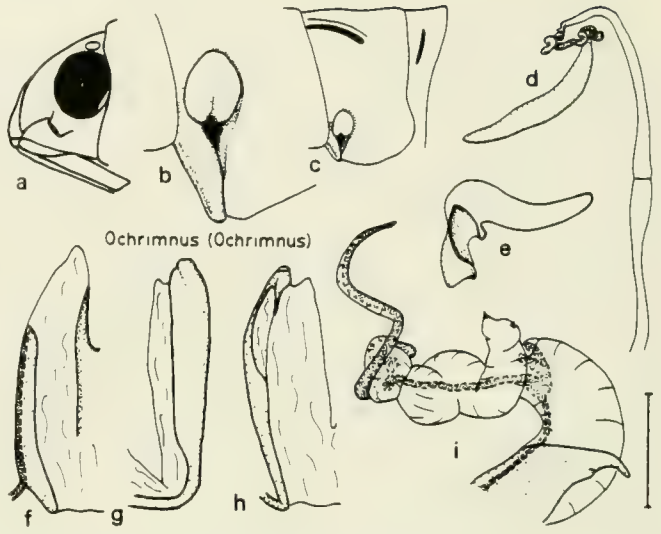


Fig. 17. *Ochrimnus* (*Ochrimnus*) *collaris* (Fabricius). a. Head. b. Ostiolar peritreme and evaporative area. c. Metapleuron. d. Spermatheca. e. Left clasper, right lateral view. f-h. Ovipositor, left valvula and connecting membrane: f, first valve, ventral view; g, second valve, lateral view; h, second valve, ventral view. i. Partially inflated aedeagus, left lateral view. Scale (mm): a,c = 1.0; b,d,f-i = 0.5; e = 0.375.

lateral fovea distinct posteriorly. *Hemelytron* surpassing apex of abdomen. *Metapleuron* (figs. 17b,c) with posterior margin straight or slightly convex, posterior margin of acetabula produced slightly posteriorly. *Abdomen* with sternum VI of female about two-thirds as long medially as laterally. *GENITALIA.* — *Clasper* (fig. 17e) with blade at acute angle to shank, usually much narrower than shank over most of its length, moderately to strongly curved, somewhat laterally flattened; posterior projection obsolete, at most represented by an indistinct bulge; shank posterior ridge distinct, with interior projection well developed, fingerlike, inserted near juncture with blade. *Aedeagus* (fig. 17i) with conjunctiva short with small, unarmed, subapical, lateral lobes; vesica with single basal lobe bearing sclerotized spines apically, moderately, asymmetrically swollen distad of basal lobe without subapical lobe or spine; apical process of secondary gonopore short, acute; phallotheca without ridges, process elongate, acute, with small secondary projection at base. *Spermatheca* (fig. 17d) with long slender basal tube, apical bulb very slender but still much broader than adjacent tube. *Ovipositor* moderately long, moderately broad; first valve (fig. 17f) with connecting membrane extending beyond apex of valvula by about half length of valvula, cleft to about three-fifths distance to base, Y-sclerite distinct, arms not reaching apex of cleft; second valve (figs. 17g,h) with connecting membrane cleft to about one-third distance to base, a short apical projection at each side of cleft not reaching level of apex of valvula, valvula flattened dorsally, swollen ventrally. *COLOR.* — *Head* brown except buccula pale yellow. *Pronotum* usually predominantly orange, occasionally predominantly dark brown. *Scutellum* dark brown to black except extreme apex and sometimes lateral margins apically pale yellow. *Hemelytron* brown with or without contrasting light veins; membrane dark brown with narrow lateral and apical margins white. *Thoracic pleura* dark brown to black except acetabulae and posterior margins pale yellow and usually posterior part of prosternum orange. *Abdomen* ventrally dark brown to black except lateral margins usually pale yellow.

DISTRIBUTION. Six of the eight species in this subgenus are restricted to islands of the Caribbean and adjacent southern Florida.

There is some overlap in their ranges. The remaining two species have very limited distributions on the west coast of Mexico and Guatemala.

COMMENTS. Members of *Ochrimnus* (*Ochrimnus*) are similar in general appearance to those of *O.* (*Parochrimnus*) but are much more robust and do not display the π-shaped dark pronotal macula characteristic of species belonging to that group. The short, sparse, dorsal pubescence separates species of this subgenus from those of other *Ochrimnus* subgenera.

Ochrimnus (Orthochrimnus) new subgenus
(Fig. 18)

Type species: *Stalagmostethus neotropicalis* Kirkaldy, 1909.

Included species: *Ochrimnus* (*Orthochrimnus*) *cinctipennis* (Stål), 1858 (*Lygaeus*); *Ochrimnus* (*Orthochrimnus*) *neotropicalis* (Kirkaldy), 1909 (*Stalagmostethus*); *Ochrimnus* (*Orthochrimnus*) *nitidulus* Brailovsky, 1982a (*Ochrimnus*); *Ochrimnus* (*Orthochrimnus*) *testatus* Brailovsky, 1982a (*Ochrimnus*).

Structure as in generic description with the following additions. *BODY.* Slender; hairs short, fine, decumbent, sparse dorsally, denser on abdominal venter. Length 4.0-6.0mm. *Head* (fig. 18a) strongly declivent; distance between ocelli about seven times distance from ocellus to eye; buccula moderately produced, ventral margin moderately convex. *Pronotum* subquadrate; with posterior width about 1.3 times anterior width; median length about 0.9 times anterior width; anterior margin raised, beaded laterally; posterior margin slightly sinuate or convex; lateral margins straight and subparallel anteriorly, straight and angled slightly anteromediad posteriorly. *Scutellum* with length about 0.8 times width; lateral fovea becoming indistinct posteriorly. *Hemelytron* usually surpassing apex of abdomen, occasionally shorter. *Metapleuron* (figs. 18b,c) with posterior margin directed slightly anterodorsally, straight or slightly concave, posterior margin of acetabula produced slightly posteriorly. *Abdomen* with sternum VI of female half to two-thirds as long medially as laterally. *GENITALIA.* — *Clasper* (fig. 18h) with blade about evenly broad throughout except for extreme apex; posterior projection at most a slight swelling; interior projection attached at posterior margin of inner face, line of attachment subparallel with posterior margin of shank, projection broad, flat, often widest apically, bent strongly at posterior end so that it runs parallel to the blade with apex anterior. *Aedeagus* (fig. 18i) with conjunctiva short, without lateral or dorsal subapical lobes; vesica with single basal lobe bearing two apical spines and a subapical lobe bearing a single spine, otherwise moderately, asymmetrically swollen; ring sclerite moderately developed, without projections; apical process of secondary gonopore obsolete; phallotheca without ridges, process elongate, scoop-shaped. *Spermatheca* (fig. 18d) with moderately long, slender basal tube; apical bulb elongate, very narrow, scarcely thicker than adjacent tube. *Ovipositor* short; first valve (fig. 18e) with connecting membrane extending beyond apex of valvula by about half length of valvula, cleft medially to about level of apex of valvula, a broad, low projection at base of cleft, Y-sclerite absent; second valve (figs. 18f,g) with connecting membrane not distinctly cleft, with low, broad medial projection, valvula apically with flat projection along dorsal margin. *COLOR.* — *Head* either black except pale bucculae or pale anterior to eyes. *Pronotum* black with yellow margins. *Scutellum* dark brown to black except apex pale yellow. *Hemelytron* black except costal and apical margins variably yellow; membrane dark brown except apical and lateral margins narrowly white. *Thoracic pleura* dark brown to black except anterior margin of propleuron, posterior margins of all pleura, and acetabulae pale yellow. *Abdomen* ventrally of females a somewhat mottled brown, of males yellow medially with dark brown margins.

DISTRIBUTION. This subgenus is primarily South American. One species (*O.* (*Orthochrimnus*) *neotropicalis*) occurs from northern South America to southern Costa Rica. The remaining species range from central Peru and Brazil to central Argentina.

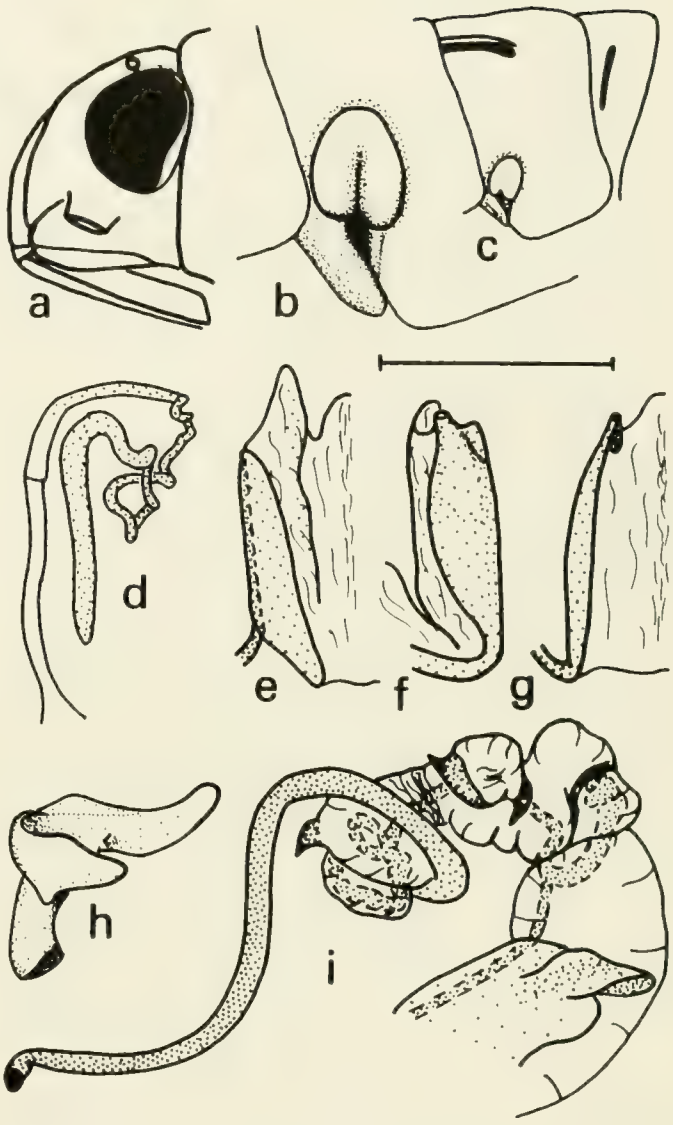


Fig. 18. *Ochrimnus* (*Orthochrimnus*) *neotropicalis* (Kirkaldy). a. Head. b. Ostiolar peritreme and evaporative area. c. Metapleuron. d. Spermatheca. e-g. Ovipositor, left valvula and connecting membrane: e, first valve, ventral view; f, second valve, lateral view; g, second valve, ventral view. h. Left clasper, right lateral view. i. Partially inflated aedeagus, left lateral view. Scale (mm): a,c = 1.0; b,d-g = 0.5; h,i = 0.375.

COMMENTS. The name *Orthochrimnus* is from the Greek and refers to the straight-sided appearance of members of the genus, a result of the subquadrate pronotum.

Members of *Ochrimnus* (*Orthochrimnus*) are easily separated from those of other subgenera of *Ochrimnus* by their almost quadrate pronota. Their coloration is reminiscent of *O.* (*Aglaochrimnus*) species, but members of that subgenus are much larger and usually have red abdominal venters.

Ochrimnus (Parochrimnus) new subgenus
(Fig. 19)

Type species: *Lygaeus carnosulus* Van Duzee, 1914.

Included species: *Ochrimnus* (*Parochrimnus*) *barberi* (Slater), 1964a (*Ochrostomus*); *Ochrimnus* (*Parochrimnus*) *carnosulus* (Van Duzee), 1914 (*Lygaeus*); *Ochrimnus* (*Parochrimnus*) *chontalensis* (Distant), 1893 (*Lygaeus*); *Ochrimnus* (*Parochrimnus*) *consanguinitas* (Distant), 1882 (*Lygaeus* (*Melanocoryphus*)); *Ochrimnus* (*Parochrimnus*) *cophinus* Brailovsky, 1982a (*Ochrimnus*); *Ochrimnus* (*Parochrimnus*) *dallasi* (Guérin-Méneville), 1857 (*Lygaeus*); *Ochrimnus* (*Parochrimnus*) *foederatus* (Van Duzee), 1929 (*Lygaeus* (*Ochrostomus*)); *Ochrimnus* (*Parochrimnus*) *lineoloides* (Slater), 1964a (*Ochrostomus*) = *Lygaeus lineola* Dallas, 1852, preocc. fide Slater, 1964a; *Ochrimnus* (*Parochrimnus*) *obsoletus* (Stål), 1858 (*Lygaeus*); *Ochrimnus* (*Parochrimnus*) *sagax* Brailovsky, 1982a (*Ochrimnus*); *Ochrimnus* (*Parochrimnus*) *scalprum* Brailovsky, 1982a (*Ochrimnus*); *Ochrimnus* (*Parochrimnus*) *sceptrum* Brailovsky, 1982a (*Ochrimnus*); *Ochrimnus* (*Parochrimnus*) *somnus* Brailovsky, 1982a (*Ochrimnus*); *Ochrimnus* (*Parochrimnus*) *somnus mulsus* Brailovsky, 1982a (*Ochrimnus*); *Ochrimnus* (*Parochrimnus*) *succineus* Brailovsky, 1982a (*Ochrimnus*).

Structure as in generic description with the following additions. *BODY.* Moderately slender; hairs short, decumbent, moderately dense. Length 4.0-6.0mm. *Head* (fig. 19a) moderately declivent; distance between ocelli about eight times distance from ocellus to eye; buccula moderately produced, ventral margin slightly to moderately convex. *Pronotum* with posterior width about 1.7 times anterior width; medial length slightly less than anterior width; anterior margin slightly raised but not beaded laterally; posterior margin slightly convex; lateral margins almost straight, slightly indented behind callus. *Scutellum* with length about 0.66 times width; lateral fovea distinct posteriorly. *Hemelytron* reaching or surpassing apex of abdomen. *Metapleuron* (figs. 19b,c) with posterior margin directed slightly anterodorsally, slightly convex, posterior margin of acetabula slightly produced posteriorly. *Abdomen* with sternum VI of female about two-thirds as long medially as laterally. *GENITALIA.* — *Clasper* (fig. 19j) with blade much longer than shank, moderately broad basally, tapering gradually to apex, posterior projection an indistinct bulge, shank with interior projection short, subtriangular, somewhat rounded apically, attached anteriorly at juncture of blade and shank, line of attachment subparallel to blade. *Aedeagus* (figs. 19h,i) with conjunctiva short, without dorsal or lateral subapical lobes; vesica basally strongly, asymmetrically swollen, with series of stout spines oriented along major axis, subapically with large single spine borne on a small lobe; apical process of secondary gonopore obsolete; phallotheca without ridges, process elongate, slender, slightly bent, acute apically. *Spermatheca* (fig. 19g) with moderately long slender basal tube; apical bulb narrow, moderately long, distinctly thicker than adjacent tube. *Ovipositor* moderately elongate; first valve (fig. 19d) with connecting membrane extending only slightly beyond apex of valvula, cleft to about half distance to base, Y-sclerite represented by a narrow sclerite along basal half of lateral margin of cleft; second valve (figs. 19e,f) with connecting membrane cleft medially to about half distance to base, without apical projection at each side of cleft, valvula slightly swollen longitudinally along ventral margin, flattened along dorsal margin. *COLOR.* — *Head* usually primarily dark brown to black with buccula and rounded macula on vertex ocher, occasionally with more extensive pale markings or lacking ocher mark on vertex. *Pronotum* ocher or orange, usually with extensive dark longitudinal markings to either side of midline, markings often connected at anterior ends. *Scutellum* dark brown to black, often with pale apical markings. *Hemelytron* usually predominantly dark brown with paler margins, often with corial veins lighter than their surroundings or occasionally predominantly orange; membrane dark brown with distinct white apical and lateral margins, these margins usually slightly wider, occasionally much wider, laterally than apically. *Thoracic pleura* usually predominantly dark brown with pale margins, occasionally predominantly pale reddish. *Abdomen* ventrally usually mottled brownish, occasionally pale reddish or with distinct pale and dark markings.

DISTRIBUTION. This subgenus ranges along the east coast of the United States from New Jersey south, and across the southern United States to northern Argentina. While many species are widely distributed, there is an almost complete split between the South American and the North and Central American faunas. The only Caribbean species is endemic to Cuba.

COMMENTS. The name *Parochrimnus* is from the Greek and indicates the similarity in general appearance between members of this and the nominate subgenus. Species of *Ochrimnus* (*Parochrimnus*) are small, rather slender, and usually have contrasting light hemelytral veins on a dark background and broad lateral light margins on the hemelytral membrane. The shape and length of the vesical spines as well as the development of the interior projection of the claspers are highly variable.

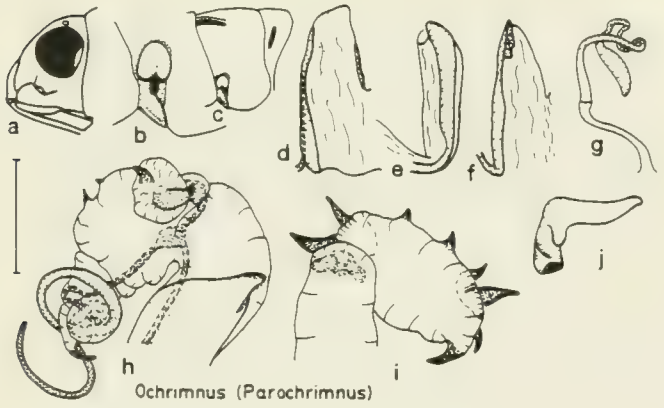


Fig. 19. *Ochrimnus* (*Parochrimnus*) *carnosulus* (Van Duzee). a. Head. b. Ostiolar peritreme and evaporative area. c. Metapleuron. d-f. Ovipositor, left valvula and connecting membrane: d, first valve, ventral view; e, second valve, lateral view; f, second valve, ventral view. g. Spermatheca. h,i. Partially inflated aedeagus: h, left lateral view; i, dorsal view. j. Left clasper, right lateral view. Scale (mm): a,c = 1.0; b,d-g = 0.5; h-j = 0.375.

Ochrimnus (Phaeochrimnus) new subgenus
(Fig. 20)

Type species: *Lygaeus pallescens* Stål, 1862.

Included species: *Ochrimnus* (*Phaeochrimnus*) *bellissimus* Brailovsky, 1982a (*Ochrimnus*); *Ochrimnus* (*Phaeochrimnus*) *dimorphopterus* Brailovsky, 1982a (*Ochrimnus*); *Ochrimnus* (*Phaeochrimnus*) *gerulus* Brailovsky, 1982a (*Ochrimnus*); *Ochrimnus* (*Phaeochrimnus*) *interstinctus* (Distant), 1882 (*Lygaeus*); *Ochrimnus* (*Phaeochrimnus*) *limbatipennis* (Stål), 1858 (*Lygaeus*); *Ochrimnus* (*Phaeochrimnus*) *luteolus* Brailovsky, 1982a (*Ochrimnus*); *Ochrimnus* (*Phaeochrimnus*) *mimulus* (Stål), 1874 (*Melanocoryphus* (*Ochrimnus*)); *Ochrimnus* (*Phaeochrimnus*) *pallescens* (Stål), 1862 (*Lygaeus*); *Ochrimnus* (*Phaeochrimnus*) *rabidus* Brailovsky, 1982a (*Ochrimnus*).

Structure as in generic description with the following additions. *BODY.* Moderately robust; hairs short, fine, decumbent, moderately dense dorsally, denser on abdominal venter. Length 5.0-7.0mm. *Head* (fig. 20a) moderately declivent; distance between ocelli about six times distance from ocellus to eye; buccula occasionally very short, moderately to strongly produced, ventral margin either moderately convex throughout or moderately convex anteriorly and strongly convex posteriorly. *Pronotum* with posterior width about 1.6 times anterior width; median length subequal to anterior width; anterior margin raised, beaded laterally; posterior margin slightly sinuate; lateral margins straight anteriorly, slightly convex posteriorly. *Scutellum* with length about 0.66 times width; lateral fovea distinct posteriorly. *Hemelytron* surpassing apex of abdomen. *Metapleuron* (figs. 20b,c) with posterior margin directed dorsoventrally, straight or slightly convex, posterior margin of acetabula some-

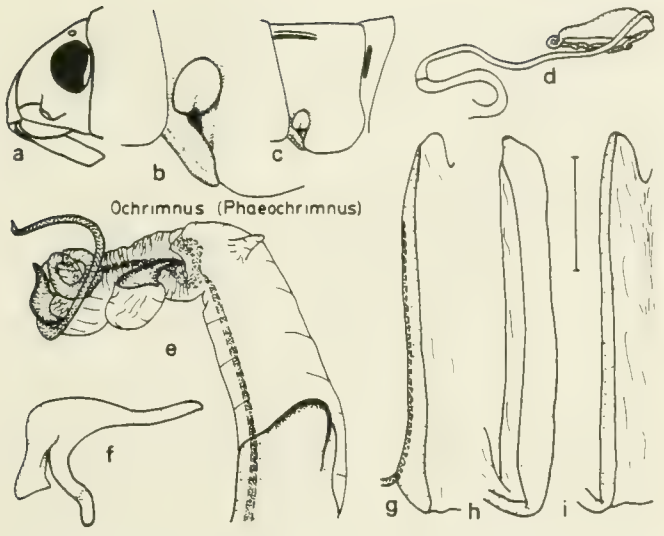


Fig. 20. a-d,f-i. *Ochrimnus* (*Phaeochrimnus*) *pallescens* (Stål). a. Head. b. Ostiolar peritreme and evaporative area. c. Metapleuron. d. Spermatheca. f. Left clasper, right lateral view. g-i. Ovipositor, left valvula and connecting membrane: g, first valve, ventral view; h, second valve, lateral view; i, second valve, ventral view. e. *Ochrimnus* (*Phaeochrimnus*) *limbatipennis* (Stål), partially inflated aedeagus, left lateral view. Scale (mm): a,c = 1.0; b,d,g-i = 0.5; e,f = 0.375.

what produced posteriorly. *Abdomen* with sternum VI of female half as long medially as laterally. *GENITALIA.* — *Clasper* (fig. 20f) with blade much longer than shank, broad, narrowing rapidly near base and then about equally broad to apex; posterior projection obsolete; interior projection elongate, often longer than shank, thin, fingerlike, inserted at juncture of blade and shank, line of attachment subparallel to blade. *Aedeagus* (fig. 20e) with conjunctiva short, without dorsal or lateral subapical lobes; vesica basally with single short lobe bearing either a stout, simple spine with a broad sclerotized base or two small spines, subapically with a single lobe bearing a single spine of varying length; apical process of secondary gonopore short, acute; phallotheca without ridges except sometimes along margin of process, process either short and broad or elongate and narrow, marginal ridge, when present, extending about half distance to base of phallotheca. *Spermatheca* (fig. 20d) with moderately long slender basal tube; apical bulb elongate, narrow, broadest subapically, distinctly broader than adjacent tube. *Ovipositor* long, slender; first valve (fig. 20g) with connecting membrane pigmented or lightly sclerotized except a narrow area at junction with valvula, extending slightly beyond apex of valvula, very slightly cleft medially, apex rounded to either side of cleft, midline and margins of cleft raised but not sclerotized to form Y-sclerite; second valve (figs. 20h,i) with connecting membrane pigmented or lightly sclerotized, slightly cleft medially, without apical projection at each side of cleft, valvula flat, slightly concave subapically. *COLOR.* — *Head* brown, except buccula pale yellow and area in front of eyes pale orange. *Pronotum* yellow except callus reddish and disc of posterior lobe brown. *Scutellum* dark to pale brown becoming pale yellow apically, sometimes tinged with red. *Hemelytron* usually pale brown with indistinct pale yellow margins, colors occasionally brighter and more sharply delineated; membrane pale brown with narrow apical and lateral margins white. *Thoracic pleura* pale brown or yellow, usually infuscated centrally. *Abdomen* ventrally mottled with yellow, red, and brown.

DISTRIBUTION. Members of this subgenus occur from the southeastern United States to southern Brazil. The majority of species are restricted to South America. The species *O.* (*Phaeochrimnus*) *pallescens*, occurring from central Mexico to Panama, and *O.* (*P.*) *limbatipennis*, occurring from southern Brazil to Costa Rica, may form a north/south species pair, for they are very similar in both external appearance and genitalic structure.

COMMENTS. The name *Phaeochrimnus* is from the Greek and refers to the indistinct dorsal markings of members of the subgenus. The elongate ovipositor distinguishes species of *Ochrimnus* (*Phaeochrimnus*) from those of other *Ochrimnus* subgenera. Though I have treated narrow, elongate ovipositors as plesiomorphic within Lygaeinae, the presence of short ovipositors in genera considered by me to be more plesiomorphic than this subgenus, and the presence of short ovipositors in other subgenera of *Ochrimnus*, indicate that the long ovipositor of *O.* (*Phaeochrimnus*) is apomorphic.

Ochrostomus Stål
(Fig. 21)

Ochrostomus Stål, 1874: 105. Type species: *Lygaeus pulchellus* Fabricius, 1794, designated by Van Duzee, 1916.

Included species: *Ochrostomus aequatorialis* (Breddin), 1912 (*Spilostethus* (*Craspeduchus*)); *Ochrostomus blumeki* Distant, 1882 (*Lygaeus* (*Craspeduchus*)); *Ochrostomus brasiliensis* (Brailovsky), 1979b (*Craspeduchus*); *Ochrostomus pulchellus* (Fabricius), 1794 (*Lygaeus*); *Ochrostomus uhleri* (Stål), 1874 (*Lygaeus* (*Craspeduchus*)).

BODY. Moderately robust; impunctate except as noted below; hairs sparse, short, decumbent, longer and denser on abdomen. Length 7.0-8.5mm. *Head* (fig. 21a) moderately declivent, vertex convex; ocellus slightly raised above surface, distance between ocelli about four times distance from ocellus to eye; faint indication of lambda-shaped impression in front of ocellus, not approaching antenniferous tubercle; buccula strongly produced, ventral margin moderately convex. *Pronotum* with posterior width about 1.3 times anterior width; medial length about equal to anterior width; anterior margin concave, not beaded, separated from callus by shallow depression with sparse, shallow punctation; pos-

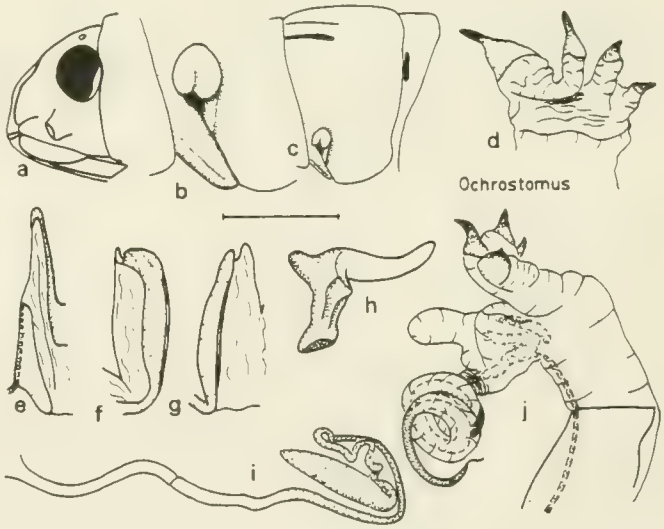


Fig. 21. *Ochrostomus pulchellus* (Fabricius). a. Head. b. Ostiolar peritreme and evaporative area. c. Metapleuron. e-g. Ovipositor, left valvula and connecting membrane: e, first valve, ventral view; f, second valve, lateral view; g, second valve, ventral view. h. Left clasper, right lateral view. i. Spermatheca. d,j. Partially inflated aedeagus: d, subapical lateral lobes, dorsal view; j, whole, left lateral view. Scale (mm): a,c = 1.0; b,d-g, i = 0.5; h,j = 0.375.

terior margin slightly convex; lateral margins slightly concave; callus slightly swollen, callar impression branched, weakly sinuate, curving toward anterior angle; narrow deeply punctate impression just behind callus interrupted medially by low carina, uninterrupted laterally. *Scutellum* with length about 0.6 times width, about apical one-fourth transversely striate; stem and arms of median carina broad; lateral fovea distinct anteriorly, becoming obsolete posteriorly. *Hemelytron* slightly surpassing apex of abdomen; corial veins distinct, slightly raised; membrane opaque. *Propleuron* divided into three parts by punctate dorsoventral impressions, median part convex. *Mesopleuron* divided into anterior and posterior parts by impunctate dorsoventral impression. *Metapleuron* (figs. 21b,c) impunctate; posterior margin angled slightly anterodorsad, almost straight, posterolateral angle sharply rounded, posterior margin of acetabula produced posteriorly; ostiolar peritreme low, distinct; evaporative area small, surrounding dorsal part of peritreme. *Abdomen* without anterolateral scars; sternum II fully exposed; sternum VI of female about two-thirds as long medially as laterally; sternum VII of female cleft to base. *GENITALIA.* — *Clasper* (fig. 21h) with shank and blade meeting at right angle; shank with inner face produced strongly inward just below junction with blade, this projection continued toward base as two longitudinal ridges, area anterior of ridges concave, posterior projection thumblike, much broader basally than apically; blade about as long as base, curved inward, twisted so that inner face is directed somewhat ventrally. *Aedeagus* (41d,j) bent before telescoping into phallotheca; conjunctiva moderately elongate, with bifid, subapical lateral lobes, each apex armed with single spine; vesica basally with elongate tubular lobe on left side, apically about evenly swollen, without lobes or spines; ring sclerite narrow, incomplete; gonoporal process short; apical process of secondary gonopore short, acute, very thin apically. *Spermatheca* (fig. 21i) with basal tube short, thin, without swelling; apical tube thin, elongate, irregularly coiled just basad of apical bulb; apical bulb narrow, elongate, acute apically, sharply bent basally. *Ovipositor* short; first valve (fig. 21e) with connecting membrane extending about length of valvula beyond apex of valvula, cleft medially to about half distance to base, Y-sclerite strongly sclerotized, stem short and broad, arms encompassing apex of membrane, valvifer triangular, valvula triangular, ramus reaching almost to apex; second valve (figs. 21f,g) with connecting membrane unpigmented, without sclerotization, extending slightly beyond apex of valvula, cleft medially to about half distance to base, valvula moderately convex, with flat dorsal and ventral projections subapically. *COLOR.* — Brightly patterned in black, yellow, and sometimes red. *Head* black except buccula pallid. *Pronotum* usually black medially with margins and sometimes an incomplete median line red or yellow. *Scutellum* black, usually pale red or yellow apically. *Hemelytron* with disc usually black, margins red or yellow; membrane dark brown with narrow white apical margin. *Thoracic pleura* dark brown to black except anterior margin of propleuron, posterior margins of all pleura, and acetabulae pale yellow. *Abdomen* ventrally either orange or black, segment VII and genital segments always black.

DISTRIBUTION. Three of the five species occur from northern South America to central Mexico or the southwestern United States. One of these species (*Ochrostomus pulchellus*) also occurs on many Caribbean islands. The remaining two species are endemic to South America, one to east-central Brazil and the other to Ecuador.

COMMENTS. Ochrostomus species are very similar in general appearance to species of *Craspeduchus* but differ greatly in genitalic structure. While *Ochrostomus* species are generally more slender than those of *Craspeduchus* and with slightly more quadrate pronota, examination of genitalia is necessary to confirm generic placement.

KEY TO SPECIES OF *OCHROSTOMUS* STÅL

1. Abdominal sterna primarily red or orange ..... *uhleri*
—Abdominal sterna primarily black 2
2. Lateral margins of abdominal sterna yellow 3
—Lateral margins of abdominal sterna black 4
3. Anterior margin of pronotum broadly yellow ..... *brasiliensis*
—Anterior margin of pronotum narrowly, indistinctly yellow ..... *aequatorialis*
4. Pronotum with thick median longitudinal pale line not reaching pale anterior margin ..... *bilimeki*
—Pronotum either without pale longitudinal median line or with very thin, indistinct line reaching pale anterior margin ..... *pulchellus*

Oncopeltus Stål
(Figs. 22, 23)

Lygaeus (*Oncopeltus*) Stål, 1868: 70. Type species: *Cimex famelicus* Fabricius, 1781, designated by Distant, 1904.
Oncopeltus Stål, 1872: 40.
Transvaalia Distant, 1892: 253, fide Distant, 1904.

Included species: See subgenera.

BODY. Robust, impunctate; dorsal hairs sparse, fine, decumbent, some species also with long, stout, dark, upright hairs on head, lateral margins and sometimes disc of pronotum, scutellum, and sometimes corium, long hairs usually densest on head and scutellum, ventral hairs moderately dense. Length 8.0-16.0mm. *Head* (figs. 22a, 23a) slightly declivent, elongate; vertex convex; ocellus distinctly raised above surface mesally and posteriorly, distance between ocelli about four to five times distance from ocellus to eye; buccula moderately produced anteriorly, low posteriorly, ventral margin moderately convex anteriorly, almost straight posteriorly. *Pronotum* with posterior width slightly more than twice anterior width; medial length about 1.2-1.3 times anterior width; anterior margin concave, slightly raised, not beaded laterally, not distinctly separated from callus; posterior margin sinuate, slightly concave medially, convex and strongly produced posteriorly on either side of scutellum; lateral margin convex except straight just behind anterolateral angle, swollen higher than callus; callus obsolete, callar impression unbranched, transverse medially, curving toward anterior angle laterally; no impression behind callus but a broad shallow longitudinal depression from callus almost to posterior margin between lateral margin and disc of posterior lobe; median carina distinct except obsolete on posterior one-third of posterior lobe. *Scutellum* with length slightly greater than width; swollen so that only apical part of stem of median carina distinct; lateral fovea represented at most by a few indistinct transverse grooves. *Hemelytron* surpassing apex of abdomen; corial veins distinct, slightly raised; membrane opaque. *Propleuron* impunctate; divided into three parts by deep dorsoventral impressions, median part convex. *Mesopleuron* impunctate; slightly convex except divided into anterior and posterior sections by distinct dorsoventral impression. *Metapleuron* (figs. 22c, 23c) impunctate; posterior margin directed dorsoventrally, slightly convex, posterior margin of acetabula not produced posteriorly; ostiolar peritreme (figs. 22b, 23b) with anterior margin of channel not higher than posterior margin, pos-

terior margin with shallow, transverse grooves, apical button ovate with long axis dorsoventral, not distinctly separated from surrounding pleuron; evaporative area small, surrounding dorsal part of peritreme, not or just reaching posterior mesopleural margin. *Abdomen* with comma-shaped anterolateral scars on sterna III through VI; sternum II fully exposed; sternum V of female sometimes produced posteriorly on midline; sternum VII of female cleft to base. *GENITALIA.* — *Clasper* (figs. 22i, 23i) with blade at moderately oblique angle to shank, moderately curved, somewhat dorsoventrally flattened, swollen subapically, posterior projection subconical or thumblike, strongly developed, shank with rooflike interior projection, median longitudinal ridge on inner face very near anterior margin, distinct groove between posterior and median ridges. *Aedeagus* (figs. 22d, 23e) bent before telescoping into phallotheca; conjunctiva short with unarmed, subapical, lateral lobes, with or without subapical dorsal lobe; vesica proximad of ring sclerite strongly swollen, without lobes or with elongate fingerlike lobe, distad of ring sclerite variable but without lobes or projections; ring sclerite well developed, without projections; gonoporal process moderately elongate. *Spermatheca* (figs. 22h, 23d) with moderately long basal tube, swelling elongate; apical tube thin, complexly coiled, apical bulb either not or only slightly differentiated from adjacent tube. *Ovipositor* short; first valve (figs. 22e, 23f) with connecting membrane extending beyond apex of valvula about valvular length, cleft to near base, Y-sclerite distinct, not reaching apex of membrane; second valve (figs. 22f,g, 23g,h) with connecting membrane cleft medially to about half distance to base, with small shoulder or projection at each side of cleft, valvula slightly convex. *COLOR.* — Marked with contrasting yellows, oranges, browns and blacks. *Head* usually either completely pale or completely dark, sometimes with both pale and dark markings, without distinct spot on vertex, buccula pale. *Pronotum* ranging from completely dark to completely pale. *Scutellum* variable, usually at least apex pale. *Hemelytron* with clavus and corium pale except usually a transverse dark median band and sometimes costal margins of corium narrowly dark; membrane dark brown to black, basal angle sometimes concolorous with adjacent part of corium, occasionally an ovate, transverse, white macula on disc near basal angle, without distinct white apical margin. *Thoracic pleura* variable, either mostly dark except margins or with propleuron completely pale and meso- and metapleura pale anteriorly and dark posteriorly. *Abdomen* ventrally either orange basally becoming dark red apically without distinct dark maculae or uniformly pale with dark anterolateral and submedian maculae, genital segments sometimes brown.

DISTRIBUTION. The nominate subgenus is pantropical while subgenus *Erythrischius* is confined to the western hemisphere.

COMMENTS. Oncopeltus belongs to that group of Lygaeinae possessing anterolateral gland openings on the abdominal sterna and a swollen scutellum without lateral foveae. It is unclear whether the two subgenera are sister groups or *Oncopeltus* (*Oncopeltus*) is rendered paraphyletic by the recognition of *O.* (*Erythrischius*). Resolution of this problem must await analysis of other eastern hemisphere genera belonging to the same group.

KEY TO WESTERN HEMISPHERE SPECIES OF *ONCOPELTUS* STÅL

1. Hemelytral membrane dark brown to black, sometimes with small white maculae; hairs of lateral pronotal margin longer, thicker, and more upright than those on hemelytra ..... (*Oncopeltus*) 2
—Basal angle of hemelytral membrane concolorous with adjacent part of corium; hairs of lateral pronotal margin similar to those of hemelytra ..... (*Erythrischius*) 12
2. Hemelytral membrane with a white discal macula 3
—Hemelytral membrane without white markings 6
3. Hemelytra dull red with at most a narrow transverse median black macula widest at costal margin ..... *sanguineolentus*
—Hemelytra yellow or orange with broad transverse median black macula and sometimes entire costal margin black 4
4. Head dorsally reddish orange ..... *spectabilis*
—Head dorsally black or red and black 5
5. Costal margin of corium entirely black ..... *sexmaculatus*
—At least that part of costal margin of corium apical to transverse black macula orange ..... *guttaloides*
6. Corium unicolored, dark orange to black 7
—Corium yellow or orange with a transverse median black macula 8
7. Scutellum entirely dark brown to black ..... *luctuosus*
—Scutellum with an orange triangular mark anteriorly on either side of midline ..... *bergianus*
8. Head dorsally dark purple to black, without contrasting lighter markings ..... *cayensis*
—Head dorsally orange or contrastingly marked with red or orange and black 9
9. Pronotum primarily orange 10
—Pronotum primarily black, light markings restricted to an anterior triangular mark to either side of midline 11
10. Light markings of hemelytra orange, concolorous with those of scutellum; black median transverse macula of corium often incomplete or absent, if complete then thickest medially; length greater than 13mm ..... *varicolor stali*
—Light markings of hemelytra pale yellow, contrasting with orange markings of pronotum; black median transverse macula of corium complete, thickest at costal margin; length less than 12.5mm ..... *femoralis*
11. Length at most 12mm; transverse black median macula of corium distinctly widest at costal margin ..... *pictus*
—Length at least 13mm; transverse black median macula of corium at most slightly widest at costal margin ..... *varicolor varicolor*
12. Dorsum densely covered with short fine hairs ..... *miles*
—Dorsum with only a few scattered hairs 13
13. Hemelytral membrane with a white mark just basad of center 14
—Hemelytral membrane without white markings 16
14. Lateral margin of posterior pronotal lobe orange ..... *aulicus*
—Lateral margin of posterior pronotal lobe dark brown to black 15
15. Rostral segment II much shorter than III ..... *longirostris*
—Rostral segments II and III subequal ..... *semilimbatus*

16. Lateral margin of posterior pronotal lobe yellow or orange 17
—Lateral margin of posterior pronotal lobe dark brown to black 18
17. Lateral margin of anterior pronotal lobe slightly redder than lateral margin of posterior lobe; length less than 12mm ..... *sandarachatus*
—Lateral margins of anterior and posterior pronotal lobes concolorous; length usually greater than 12mm ..... *fasciatus*
18. Light markings of pronotum infuscated, indistinctly separated from dark markings ..... *zonatus*
—Light markings of pronotum not infuscated, sharply separated from dark markings 19
19. Dark markings of anterior and posterior pronotal lobes connected by a median longitudinal line ..... *cingulifer*
—Dark markings of anterior and posterior pronotal lobes not connected medially ..... *unifasciatellus*

Oncopeltus (Erythrischius) Stål
(Fig. 22)

Oncopeltus (*Erythrischius*) Stål, 1874: 102. Type species: *Lygaeus fasciatus* Dallas, 1852, designated by Van Duzee, 1916.

Included species: *Oncopeltus* (*Erythrischius*) *aulicus* (Fabricius), 1775 (*Cimex*) = *Lygaeus hamatus* Herrich-Schäffer, 1847, fide Herrich-Schäffer, 1850; *Oncopeltus* (*Erythrischius*) *cingulifer* Stål, 1874; *Oncopeltus* (*Erythrischius*) *fasciatus* (Dallas), 1852 (*Lygaeus*); *Oncopeltus* (*Erythrischius*) *longirostris* Stål, 1874; *Oncopeltus* (*Erythrischius*) *miles* (Blanchard), 1852 (*Lygaeus*); *Oncopeltus* (*Erythrischius*) *sandarachatus* (Say), 1831 (*Lygaeus*); *Oncopeltus* (*Erythrischius*) *semilimbatus* Stål, 1874; *Oncopeltus* (*Erythrischius*) *unifasciatellus* Slater, 1964a = *Lygaeus unifasciatus* Hahn, 1834, preocc. fide Slater, 1964a; *Oncopeltus* (*Erythrischius*) *zonatus* (Erichson), 1848 (*Lygaeus*).

Structure as in generic description with the following additions. Dorsum without long, coarse, dark, upright hairs, occasionally with moderately long and dense dorsal hairs. *Head* (fig. 22a) with distance between ocelli about five times distance from ocellus to eye; buccula moderately produced anteriorly, low posteriorly, ventral margin moderately convex anteriorly, slightly concave posteriorly. *Pronotum* with medial length about 1.3 times anterior width. *Abdomen* with sternum V of female produced posteriorly at midline to cover part of sternum VI, almost twice as long medially as laterally. *GENITALIA.* — *Clasper* (fig. 22i) with posterior projection subconical, shank with groove between posterior and median longitudinal ridges narrow. *Aedeagus* (fig. 22d) with subapical, lateral lobes short, laterally directed; with distinct subapical dorsal lobe; vesica proximad of ring sclerite with elongate, fingerlike lobe on right side, distad of ring sclerite flattened and scored with numerous transverse lines, without projections; ring sclerite broad; apical process of secondary gonopore swollen, with elongate vermiform apex; phallotheca without fine ridges on disc, process short, flared laterally, with indistinct ridge along apical margin. *Spermatheca* (fig. 22h) with apical bulb elongate, slightly thicker than adjacent tube, apex bluntly rounded. *Ovipositor* with first valve (fig. 22e) with connecting membrane extending beyond apex of valvula slightly more than valvular length, arms of Y-sclerite reaching beyond level of apex of valvula; second valve (figs. 22f,g) with small apical projection at each side of cleft. *COLOR.* — As in generic description with the following exceptions. *Head* usually pale except tylus and around eyes. *Pronotum* usually pale laterally, dark anteriorly, posteriorly, and medially, sometimes dark medial markings interrupted behind callus. *Hemelytron* with clavus and corium pale except transverse dark median band; membrane dark except basal angle concolorous with adjacent part of corium and occasionally an elongate transverse, white macula on disc near pale basal angle. *Thoracic pleura* dark except narrow anterior margin of propleuron and all acetabulae and posterior margins. *Abdomen* with sterna II through VI mostly pale, III through VI with dark maculae surrounding anterolateral scars and with dark maculae of varying size to either side of midline, occasionally meeting ventrally, sternum VII and genital segments dark.

DISTRIBUTION. Species in this subgenus occur from southern Canada to central Argentina. As the subgenus is very difficult taxonomically at the species level, there is considerable doubt as to the actual distribution of many species. The majority of species appear to occur from central Mexico to northern South America. Two species have very limited distributions, one in Guyana and the other in north-central Chile. At least six of the nine recognized species have been reported from Caribbean islands as well as the mainland, indicating a high degree of vagility.

COMMENTS. Subgenus *Erythrischius* is restricted to the western hemisphere. The continuation of the corial color pattern onto the basal angle of the hemelytral membrane is diagnostic for all species of the subgenus, as is the posterior extension of abdominal sternum V of females. *Oncopeltus* (*Erythrischius*) seems more plesio-

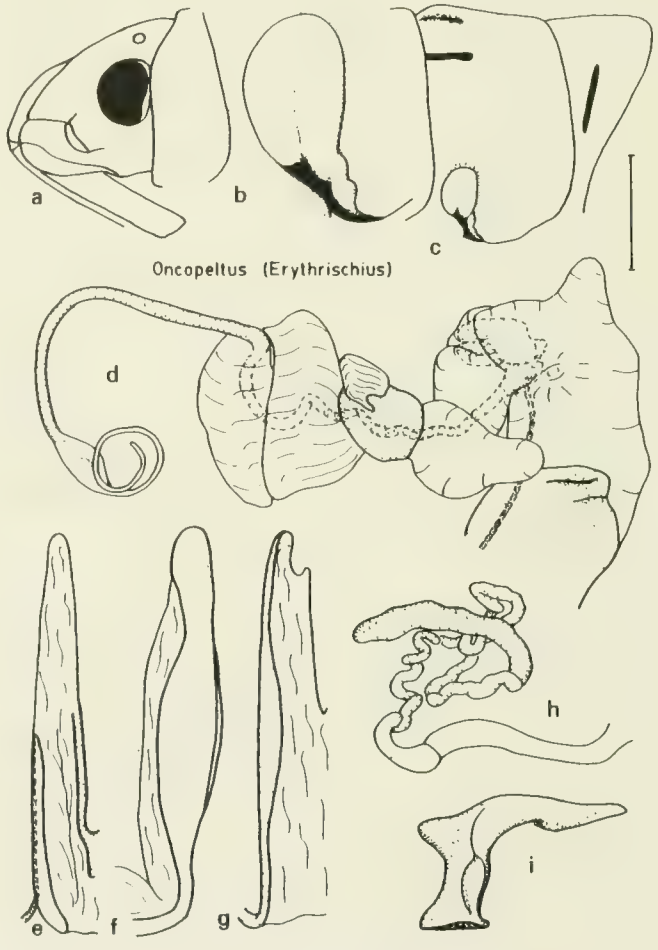


Fig. 22. *Oncopeltus* (*Erythrischius*) *fasciatus* (Dallas). a. Head. b. Ostiolar peritreme and evaporative area. c. Metapleuron. d. Partially inflated aedeagus, left lateral view. e-g. Ovipositor, left valvula and connecting membrane: e, first valve, ventral view; f, second valve, lateral view; g, second valve, ventral view. h. Spermatheca. i. Left clasper, right lateral view. Scale (mm): a,c = 1.0; b,d-h = 0.5; i = 0.375.

morphic than the nominate subgenus in such characters as the distinct apical bulb of the spermatheca and hard abdominal sternites.

Oncopeltus (Oncopeltus) Stål
(Fig. 23)

Lygaeus (*Oncopeltus*) Stål, 1868: 70. Type species: *Cimex famelicus* Fabricius, 1781, designated by Distant, 1904.
Oncopeltus Stål, 1872: 40.
Transvaalia Distant, 1892: 253.
Oncopeltus (*Oncopeltus*) Stål, 1874: 98.

Included species (western hemisphere only): *Oncopeltus* (*Oncopeltus*) *bergianus* Kirkaldy, 1909 = *Oncopeltus stalii* Berg, 1883, preocc. fide Kirkaldy, 1909; *Oncopeltus* (*Oncopeltus*) *cayensis* Torre-Bueno, 1944 (*Oncopeltus* (*Erythrischius*)); *Oncopeltus* (*Oncopeltus*) *femoralis* Stål, 1874 = *Lygaeus quadriguttatus* Dallas, 1852, preocc. fide Stål, 1874; *Oncopeltus* (*Oncopeltus*) *guttaloides* Slater, 1964a = *Lygaeus gutta* Herrich-Schäffer, 1843, preocc. fide Slater, 1964a; *Oncopeltus* (*Oncopeltus*) *luctuosus* Stål, 1867 (*Lygaeus*); *Oncopeltus* (*Oncopeltus*) *pictus* Van Duzee, 1907; *Oncopeltus* (*Oncopeltus*) *sanguineolentus* Van Duzee, 1914; *Oncopeltus* (*Oncopeltus*) *sexmaculatus* Stål, 1874; *Oncopeltus* (*Oncopeltus*) *spectabilis* Van Duzee, 1909; *Oncopeltus* (*Oncopeltus*) *varicolor* Fabricius, 1794 (*Lygaeus*) = *Lygaeus alternans* Herrich-Schäffer, 1843, fide Stål, 1874; *Oncopeltus* (*Oncopeltus*) *varicolor stali* Distant, 1882.

Structure as in generic description with the following additions. Head, lateral margins and sometimes disc of pronotum, scutellum and sometimes corium with long, stout, dark, upright hairs, usually densest on head and scutellum. Length 9.0-16.0mm. *Head* (fig. 23a) with distance between ocelli about four times distance from ocellus to eye; buccula with ventral margin moderately convex anteriorly, almost straight posteriorly. *Pronotum* with medial length about 1.2 times anterior width. *Abdomen* with sternum V of female not produced posteriad medially, about equally long medially and laterally. *GENITALIA.* — *Clasper* (fig. 23i) with blade at slightly oblique angle to shank; posterior projection thumblike; shank with groove between posterior and median longitudinal ridges very broad. *Aedeagus* (fig. 23e) with subapical lateral lobes large, subconical, dorsally directed, without subapical dorsal lobe; vesica proximad of ring sclerite strongly, asymmetrically swollen but without lobes or spines, distad of ring sclerite strongly swollen, not flattened; ring sclerite narrow; apical process of secondary gonopore short, belled; phallotheca with raised area bearing numerous fine ridges on disc, apical margin with flange over about dorsal half, process very short. *Spermatheca* (fig. 23d) with apical bulb not differentiated from adjacent tube. *Ovipositor* with first valve (fig. 23f) with connecting membrane extending beyond apex of valvula by slightly less than valvular length, arms of Y-sclerite not extending as far as apex of valvula; second valve (figs. 23g,h) without apical projection at each side of cleft. *COLOR.* — As in generic description with the following exceptions. *Head* usually dark purple to black, sometimes gula and markings on dorsum pale. *Pronotum* ranging from completely dark to completely pale, dark markings usually appearing first along all margins and midline and then increasing until only a small triangular macula to either side of midline anteriorly pale. *Hemelytron* with clavus and corium pale except transverse median band and sometimes narrow costal margins of corium dark; membrane including basal angle dark brown to black, occasionally with an ovate, transverse, white macula on disc near basal angle. *Thoracic pleura* variable, propleuron usually completely pale, meso- and metapleuron usually pale anteriorly and dark posteriorly. *Abdomen* ventrally orange basally, becoming dark red apically, without distinct dark maculae, genital segments sometimes brown.

DISTRIBUTION. In the western hemisphere species of this subgenus occur from the southern United States to central Argentina. These species are generally more restricted in their ranges than are those of *Oncopeltus* (*Erythrischius*). Only one species occurs in both North and South America. Three species are restricted to South America, two species are endemic to Jamaica, one species is restricted to southern Florida and the Bahama Islands, one species is restricted to the southwestern United States and northwestern Mexico, and two species range from the southern United States to Honduras and are reported from Cuba and Jamaica.

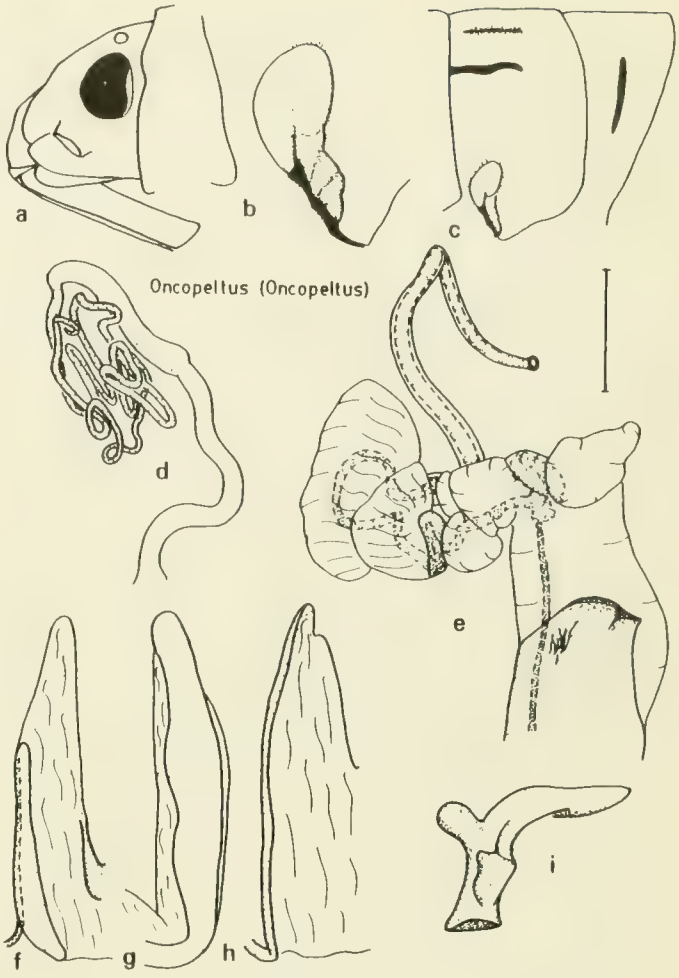


Fig. 23. *Oncopeltus* (*Oncopeltus*) *sanguineolentus* Van Duzee. a. Head. b. Ostiolar peritreme and evaporative area. c. Metapleuron. d. Spermatheca. e. Partially inflated aedeagus, left lateral view. f-h. Ovipositor, left valvula and connecting membrane: f, first valve, ventral view; g, second valve, lateral view; h, second valve, ventral view. i. Left clasper, right lateral view. Scale (mm): a,c = 1.0; b,d-h = 0.5; i = 0.375.

COMMENTS. The swollen pronotum and scutellum, combined with the numerous long, stiff, upright hairs on head, pronotum, and scutellum, are diagnostic of *Oncopeltus* (*Oncopeltus*). In pinned specimens the abdomen is always shrunken and distorted, indicating that the cuticle is very soft, a neotenic condition not shared with subgenus *Erythrischius*.

Orsillacis Barber
(Fig. 24)

Orsillacis Barber, 1914: 169. Type species: *Orsillacis producta* Barber, 1914, monobasic.

Included species: *Orsillacis producta* Barber, 1914.

BODY. Slender, moderately elongate; entire pronotum, thoracic pleura, and lateral scutellar fovea strongly punctate; hairs mod-

erately dense dorsally except on disc of posterior pronotal lobe, densest and longest on hemelytron; hairs of abdominal venter short, sparse, interspersed medially with scattered, long, upright hairs. Length 6.5-7.0mm. *Head* (fig. 24a) porrect; tylus extending at least as far as apex of antennal segment I; vertex almost flat; ocellus set on distinct protuberance, least distinct laterally, directed slightly anterolaterally, distance between ocelli about five times distance from ocellus to eye; buccula scarcely produced, ventral margin almost straight. *Pronotum* deeply, coarsely punctate except immediately around callar impressions and on extreme posterior margin; posterior width about 1.7 times anterior width; median length slightly less than anterior width; anterior margin slightly concave, not raised, separated from callus by very narrow flat area paralleling margin; posterior margin convex medially, sinuate laterally; lateral margins slightly convex anteriorly and posteriorly, indented at postcallar impression; callus distinct, callar impressions very thick, with vestigial branch mesally; postcallar impression distinct, interrupted medially and to either side of midline by broad low carinae; posterior lobe almost flat. *Scutellum* with length about 0.8 times width; stem and arms of median carina low, arms broader than stem; lateral fovea indistinct, represented by confluent deep, coarse punctures. *Hemelytron* considerably surpassing apex of abdomen; corial veins distinct, slightly raised; membrane transparent. *Propleuron* coarsely punctate; divided into three parts by dorsoventral impressions; middle part convex, swollen dorsally. *Mesopleuron* coarsely punctate; impressed dorsoventrally near posterior margin. *Metapleuron* (fig. 24c) coarsely punctate; impressed dorsoventrally near posterior margin; posterior margin directed posteroventrally, slightly concave, posterior margin of acetabula slightly produced posteriorly; ostiolar peritreme (fig. 24b) strongly produced, with anterior margin of channel higher than posterior margin, apical button slightly elongate anteroposteriorly; evaporative area large, surrounding dorsal part of peritreme posteriorly, extending along both sides of meso-metapleural boundary about half distance to dorsal margins and covering posterior part of mesopleural acetabula. *Abdomen* without anterolateral scars; sternum II fully exposed; posterior margin of sternum IV of female almost touching sternum VII; sterna V and VI of female very short medially, VI not measurable, V about one-sixteenth as long medially as laterally; sternum VII of female very long medially, cleft to base. *GENITALIA.* — *Clasper* (fig. 24f) with blade at about right angle to shank, short, broad, flat, slightly curved, twisted so that inner face is directed somewhat ventrally; posterior projection low; shank broad, flattened posteriorly, with short rooflike interior projection, inner face slightly concave between posterior and medina ridges. *Aedeagus* (fig. 24e) telescoped directly into phallotheca; conjunctiva elongate, without subapical lobes; vesica about evenly swollen throughout, without lobes or spines; ring sclerite absent; helicoid process complete; gonoporal process short; secondary gonopore without distinct process. *Spermatheca* (fig. 24d) with short basal tube, swelling forming a distinct bulb, rounded basally, slightly constricted medially, widened to form an apical cup, about apical half pigmented; apical tube pigmented, with a basal bulb resting in cup, a moderately long tubular section, about as thick as basal tube; apical bulb small, globose. *Ovipositor* narrow, elongate; first valve (fig. 24g) with membrane only slightly cleft medially, not extending beyond apex of valvula, without Y-sclerite; second valve (figs. 24h,i) with membrane only slightly cleft medially, without projections at each side of cleft, without noticeable pigmented or sclerotized areas, valvula flat, subacute apically. *COLOR.* — Light brown with dark brown punctation. Hemelytral membrane transparent, tinged with brown basally.

DISTRIBUTION. The single species is known only from southern Arizona.

COMMENTS. The single species of *Orsillacis* is the only western hemisphere lygaeine to display punctures within the lateral foveae of the scutellum. The many plesiomorphic features are shared with genera from the eastern hemisphere rather than with other western hemisphere genera. I believe it to be a relict species, perhaps representing the most primitive lygaeine lineage.

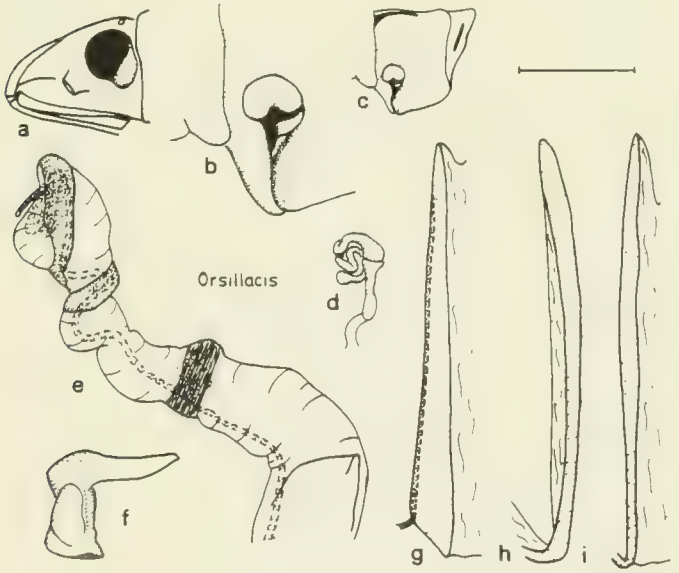


Fig. 24. *Orsillacis producta* Barber. a. Head. b. Ostiolar peritreme and evaporative area. c. Metapleuron. d. Spermatheca. e. Partially inflated aedeagus, left lateral view. f. Left clasper, right lateral view. g-i. Ovipositor, left valvula and connecting membrane: g, first valve, ventral view; h, second valve, lateral view; i, second valve, ventral view. Scale (mm): a,c = 1.0; b,d,g-i = 0.5; e,f = 0.375.

Oxygranulobaphus Brailovsky
(Fig. 25)

Oxygranulobaphus Brailovsky, 1982b: 265. Type species: *Oxygranulobaphus willinki* Brailovsky, 1982b, monobasic.

Included species: *Oxygranulobaphus willinki* Brailovsky, 1982b.

BODY. Robust; impunctate except on most of pronotum, prosternum, and propleuron; hairs short, decumbent, moderately dense dorsally, denser on venter. Length 6.5-7.5mm. *Head* (fig. 25a) moderately declivent; vertex moderately convex; ocellus distinctly raised above surface mesally and posteriorly, distance between ocelli about eight times distance from ocellus to eye; buccula moderately produced, ventral margin moderately convex. *Pronotum* with posterior width about 1.7 times anterior width; medial length slightly greater than anterior width; anterior margin concave, raised most strongly laterally, not beaded, separated from callus by coarsely punctate depression; posterior margin slightly convex; lateral margins almost straight, slightly indented just behind callus; callus distinct, callar impressions branched at mesal ends, sinuate, curving evenly toward anterior pronotal angles; shallow depression behind callus interrupted by low median carina, distinctly, coarsely punctate; posterior lobe coarsely punctate, fewer punctures near posterior margin. *Scutellum* with length about 0.6 times width; stem and arms of median carina about equally broad; lateral fovea distinct anteriorly becoming obsolete posteriorly, bottom smooth. *Hemelytron* reaching or slightly surpassing apex of abdomen; corial veins distinct, slightly raised; membrane opaque. *Propleuron* divided into three parts by shallow dorsoventral impressions; anterior and posterior parts flat, densely, coarsely punctate; central part slightly convex with a few indistinct punctures. *Mesopleuron* divided into two parts by shallow dorsoventral impression; anterior part slightly convex, impunctate; posterior part flat, with a few indistinct punctures. *Metapleuron* (fig. 25c) impunctate, posterior margin directed slightly posterolaterally, concave, posterior margin of

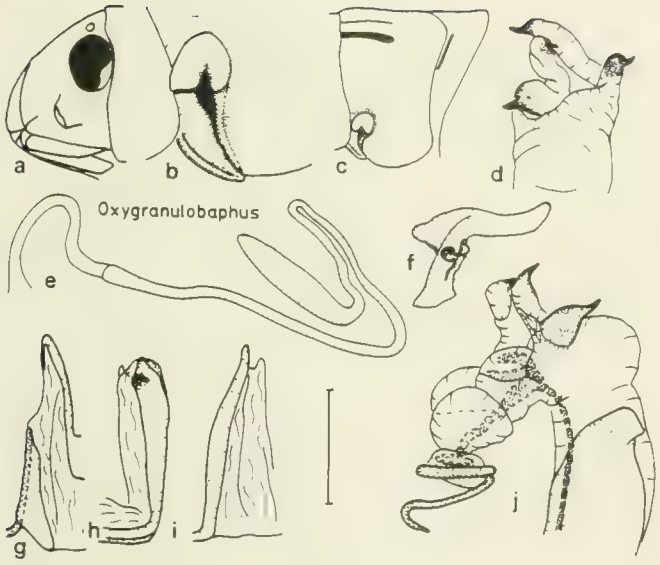


Fig. 25. *Oxygranulobaphus willinki* Brailovsky. a. Head. b. Ostiolar peritreme and evaporative area. c. Metapleuron. e. Spermatheca. f. Left clasper, right lateral view. g-i. Ovipositor, left valvula and connecting membrane: g, first valve, ventral view; h, second valve, lateral view; i, second valve, ventral view. d,j. Partially inflated aedeagus: d, apex of conjunctiva, dorsal view; j, whole, left lateral view. Scale (mm): a,c = 1.0; b,e,g-i = 0.5; d,f,j = 0.375.

acetabula produced slightly posteriad; ostiolar peritreme (fig. 25b) with anterior margin of channel higher than posterior margin, apical button rounded, ventral margin anteriorly produced, distinctly separated from surrounding pleuron anteriorly as well as dorsally and posteriorly; evaporative area moderate in size, surrounding apex of peritreme. *Abdomen* without anterolateral scars; sternum II fully exposed; sternum VI of female about half as long medially as laterally; sternum VII of female cleft to base. *GENITALIA.* — *Clasper* (fig. 25f) with blade at about right angle to shank, about as long as shank, curved, somewhat flattened, twisted so that inner face is somewhat ventrally directed; posterior projection well developed, directed posteriorly, very broad basally, conical; shank with strongly developed rooflike interior projection hooked apically almost to touch longitudinal ridge, forming a circular opening, inner face anterior of ridge with a shallow groove and a short acute ridge near juncture with blade. *Aedeagus* (fig. 25d,j) bent before telescoping into phallotheca; conjunctiva short, with lateral subapical lobes bifid, each apex bearing single stout spine; vesica basally with elongate lobe on left side, otherwise strongly, asymmetrically swollen; ring sclerite obsolete; gonoporal process moderately elongate; apical process of secondary gonopore short, acute. *Spermatheca* (fig. 25e) with basal tube short, without swelling; apical tube very long, irregularly coiled at junction with apical bulb; apical bulb somewhat elongate and narrowed, apex bluntly rounded. *Ovipositor* short, slender; first valve (fig. 25g) with connecting membrane cleft to about half distance to base, extending about two-thirds length of valvula beyond apex of valvula, Y-sclerite strongly sclerotized, stem short, arms encompassing apex of membrane, valvifer triangular, valvula triangular, ramus almost reaching apex; second valve (figs. 25h,i) with connecting membrane cleft almost to base, without pigmentation or sclerotized areas, an acute projection at each side of cleft not reaching level of apex of valvula, valvula slightly swollen longitudinally, with a distinct bulge subapically at dorsal margin. *COLOR.* — *Head* dark brown except pale spot on vertex. *Pronotum* medium brown. *Scutellum* dark brown. *Hemelytron* tan basally and apically, an irregular band across disc of corium and apical half of clavus dark brown; membrane dark brown except broad apical margin and basal angle white. *Thoracic pleura* brownish anteriorly, becoming somewhat orange posteriorly. *Abdomen* ventrally brownish orange except sterna VII and genital segments dark brown.

DISTRIBUTION. The single species occurs from central Bolivia to central Argentina.

COMMENTS. The single species of *Oxygranulobaphus* is very similar in general appearance to *Craspeduchus attrahens* Brailovsky and Barrera, which I have not seen. However, their (1984) genitalia figures for that species are quite unlike the genitalia of *Oxygranulobaphus.* The development of the inner projection of the clasper is quite unlike that of any other lygaeine.

Pseudacroleucoides Brailovsky
(Fig. 26)

Pseudacroleucoides Brailovsky, 1982b: 262. Type species: *Acroleucus vicinalis* Distant, 1882, monobasic.

Included species: *Pseudacroleucoides vicinalis* (Distant), 1882 (*Acroleucus*).

BODY. Moderately robust; impunctate except on pronotum before and behind callus and on thoracic pleura; hairs dorsally dense, moderately long, semidecumbent, interspersed with longer upright hairs on head, with longer and more decumbent hairs on abdominal venter. Length 3.5-4.0mm. *Head* (fig. 26a) strongly declivent, vertex strongly convex; ocellus raised slightly above surface mesally, distance between ocelli about eight times distance from ocellus to eye; buccula moderately produced, ventral margin slightly convex. *Pronotum* with posterior width 1.5 times anterior width; medial length slightly less than anterior width; anterior margin concave, raised laterally, separated from callus by shallow

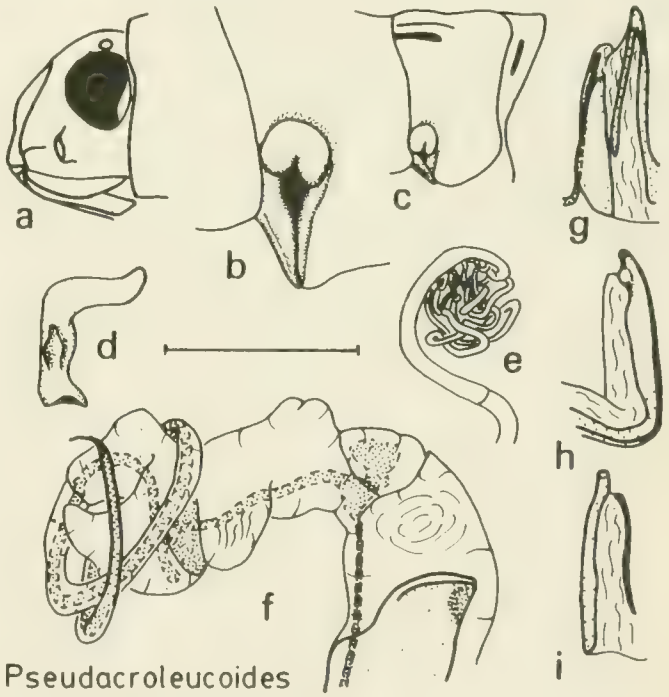


Fig. 26. *Pseudacroleucoides vicinalis* (Distant). a. Head. b. Ostiolar peritreme and evaporative area. c. Metapleuron. d. Left clasper, right lateral view. e. Spermatheca. f. Partially inflated aedeagus, left lateral view. g-i. Ovipositor, left valvula and connecting membrane: g, first valve, ventral view; h, second valve, lateral view; i, second valve, ventral view. Scale (mm): a,c = 1.0; b,e,g-i = 0.5; d,f = 0.375.

depression with coarse, shallow punctation; posterior margin slightly convex; lateral margins almost straight and angled slightly laterad from anterior angle to postcallar indentation, slightly convex and angled sharply laterad from postcallar indentation to broadly rounded humeral angles; callus indistinct, callar impressions unbranched, slightly sinuate, broadest near mesal ends; postcallar impression shallow, deeply punctate; posterior lobe convex, much higher medially than laterally, slightly impressed just inside lateral margins. *Scutellum* with length about 0.8 times width; stem and arms of median carina broad; lateral fovea deepest basally, distinct apically, bottom with indistinct transverse striae. *Hemelytron* slightly surpassing apex of abdomen; corial veins distinct, slightly raised; membrane opaque. *Propleuron* divided into three parts by dorsoventral impressions, anterior impression indistinct, posterior impression distinct; middle and posterior parts coarsely punctate. *Mesopleuron* divided into anterior and posterior parts by dorsoventral impression; coarsely punctate except posterior margin. *Metapleuron* (fig. 26c) coarsely punctate near posterior margin; posterior margin directed dorsoventrally, slightly concave, posterior margin of acetabula produced moderately posteriad; ostiolar peritreme (fig. 26b) with anterior margin of channel higher than posterior margin, apical button rounded, distinctly separated from surrounding pleuron dorsally and posteriorly; evaporative area small, surrounding dorsal part of peritreme. *Abdomen* without anterolateral scars; sternum II fully exposed; sternum VI of female about half as long medially as laterally; sternum VII of female cleft to base. *GENITALIA.* — *Clasper* (fig. 26d) with blade at about right angle to shank, strongly curved, flattened horizontally; without posterior projection; shank with short rooflike interior projection formed by joining of two longitudinal ridges. *Aedeagus* (fig. 26f) bent before telescoping into phallotheca; conjunctiva short, with moderately developed, bulbous, unarmed, subapical lateral lobes; vesica proximad of ring sclerite with low double dorsal bulge near base, distad of ring sclerite pigmented and with short hooked projection at junction with ring sclerite; ring sclerite well developed, without projections; gonoporal process elongate; apical process of secondary gonopore short, acute, with vermiform apical projection; phallothecal process with ridge along apical margin and depression near apex of dorsal margin. *Spermatheca* (fig. 26e) with basal tube short; apical tube long, thinnest and complexly coiled apically; apical bulb thin, complexly coiled, not differentiated from adjacent tube. *Ovipositor* short; first valve (fig. 26g) with connecting membrane extending beyond apex of valvula about half length of valvula, cleft almost to base, Y-sclerite completely surrounding cleft and encompassing apex of membrane, a thin, elongate sclerite extending from apex to near middle of valvula; second valve (figs. 26h,i) with membrane cleft to near base, margins of cleft strongly pigmented or sclerotized, with distinct shoulder at apex of cleft, valvula with subapical bulge at dorsal margin. *COLOR.* — *Head* black except buccula and small round spot on vertex pale yellow or white. *Pronotum* pinkish red with a large black macula on each side of posterior lobe. *Scutellum* dark brown to black, often with red or orange apex. *Hemelytron* with clavus and corium brownish black except pale yellow margins; membrane dark brown with narrow light corial margin and with white apical margin broadest at apex, becoming rapidly narrower laterally. *Thoracic pleura* pale pinkish yellow, infuscated centrally. *Abdomen* ventrally brownish.

DISTRIBUTION. The single species occurs from central Mexico to Panama.

COMMENTS. The small size and bulbous head in *Pseudacroleucoides* make the single species easy to recognize. General appearance is much like that of *Latochrimnus* species, but the aedeagus and spermatheca are most similar to those of members of *Torvochrimnus*.

Torvochrimnus Brailovsky
(Fig. 27)

Torvochrimnus Brailovsky, 1982a: 133. Type species: *Coreus striatus* Fabricius, 1803, original designation.

Included species: *Torvochrimnus kormilevi* Brailovsky, 1983b; *Torvochrimnus poeyi* (Guérin-Méneville), 1844 (*Lygaeus*) = *Lygaeus* (*Ochrostomus*) *trivittatus* Berg, 1883, preocc. fide Slater, 1964a = *Lygaeus bergi* Slater, 1964a, fide Brailovsky, 1983b = *Lygaeus* (*Ochrostomus*) *venosus* Distant, 1893, fide Barber, 1947; *Torvochrimnus striatus* (Fabricius), 1803 (*Coreus*).

BODY. Moderately robust; impunctate except pronotum before and behind callus and indistinct punctures on propleuron; hairs moderately dense, decumbent, interspersed with a few long upright hairs medially on abdominal venter. Length 4.5-8.0mm. *Head* (fig. 27a) moderately declivent, vertex almost flat; ocellus slightly raised mesally and posteriorly, distance between ocelli about five times distance from ocellus to eye; buccula moderately produced, ventral margin moderately convex, most strongly convex anteriorly. *Pronotum* with posterior width about 1.8 times anterior width; medial length slightly greater than anterior width; anterior margin raised, beaded laterally, separated from callus by shallow, coarsely punctate depression interrupted medially by faint carina; posterior margin slightly convex; lateral margins almost straight; callus low, distinct, callar impressions unbranched, moderately strongly curved; postcallar impression shallowly, coarsely punctate, interrupted to either side of midline by indistinct carina; disc of posterior lobe moderately convex, slightly higher than adjacent lateral margins. *Scutellum* with length about 0.9 times width; arms of median carina broader and higher than stem; lateral fovea shallowest apically, bottom smooth. *Hemelytron* considerably surpassing apex of abdomen; corial veins distinct basally, indistinct apically, scarcely raised; membrane opaque. *Propleuron* shallowly and indistinctly punctate; divided into three parts by indistinct dorsoventral impressions, middle part slightly convex. *Mesopleuron* impunctate; divided into two parts by shallow dorsoventral impression; impression with shallow oblique striae. *Metapleuron* (fig. 27c) impunctate; posterior margin directed dorsoventrally, slightly

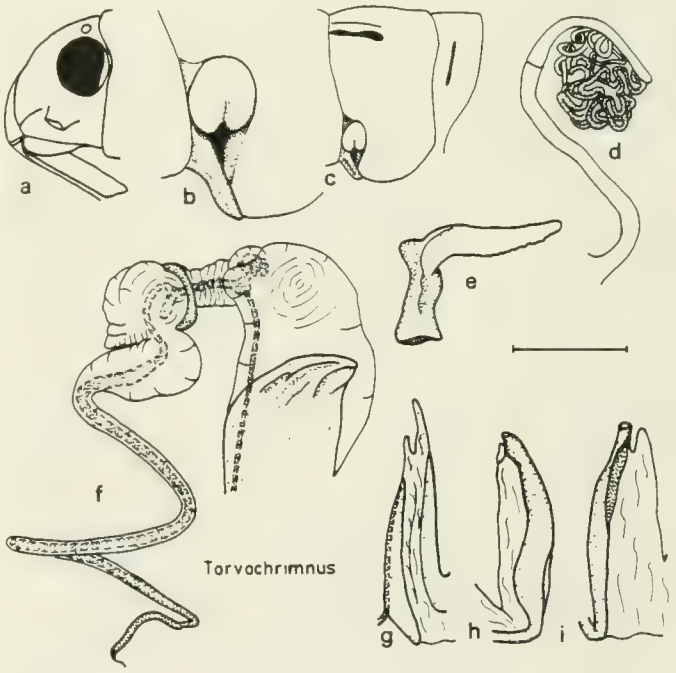


Fig. 27. *Torvochrimnus poeyi* (Guérin-Méneville). a. Head. b. Ostiolar peritreme and evaporative area. c. Metapleuron. d. Spermatheca. e. Left clasper, right lateral view. f. Partially inflated aedeagus, left lateral view. g-i. Ovipositor, left valvula and connecting membrane: g, first valve, ventral view; h, second valve, lateral view; i, second valve, ventral view. Scale (mm): a,c = 1.0; b,d,f-i = 0.5; e = 0.375.

concave, posterior margin of acetabula not produced posteriorly; ostiolar peritreme (fig. 27b) with anterior margin of channel higher than posterior margin, apical button rounded, distinct from surrounding pleuron dorsally and posteriorly; evaporative area small, surrounding dorsal part of peritreme. *Abdomen* without anterolateral scars; sternum II fully exposed; sternum VI of female about five-sevenths as long medially as laterally; sternum VII of female cleft to base. *GENITALIA.* — *Clasper* (fig. 27e) with blade meeting shank at about right angle, at least twice as long as shank, narrow, slightly curved inward along entire length, little flattened, inner and ventral surfaces coarsely rugose; posterior projection either moderately developed or obsolete; shank at least half as long as blade, without rooflike interior projection, with a single longitudinal ridge. *Aedeagus* (fig. 27f) bent before telescoping into phallotheca; conjunctiva short with short, unarmed, subapical, lateral lobes; vesica basally without distinct lobes, subapically with short membranous projection; ring sclerite complete, narrow; gonoporal process elongate; apical process of secondary gonopore short, acute, with vermiform apical projection; phallothecal process short, with series of oblique ridges converging toward apex. *Spermatheca* (fig. 27d) with basal tube long, thick; apical tube thick basally, thin and complexly coiled apically; apical bulb complexly coiled, not differentiated from adjacent tube. *Ovipositor* moderately elongate; first valve (fig. 27g) with connecting membrane extending beyond apex of valvula by about half length of valvula, cleft to about one-third distance from base to apex, a secondary cleft laterad of median cleft with longer resulting projection interior, Y-sclerite extending to about level with apex of valvula; second valve (figs. 27h,i) with connecting membrane not surpassing apex of valvula, cleft to slightly more than half distance to base, a distinct projection at apex of cleft, valvula strongly convex apically. *COLOR.* — *Head* pale brown except area around tylus and around ocellus dark brown. *Pronotum* pale brown with variably shaped dark brown maculae. *Scutellum* light brown except usually extreme base and median carina dark brown. *Hemelytron* pale brown except veins contrasting dark brown; membrane brown, without or with extremely narrow white apical margin. *Thoracic pleura* pale brown or yellow, sometimes with dark transverse maculae. *Abdomen* ventrally light brown or yellow, anterior margins of sternites often reddish.

DISTRIBUTION. The exact ranges of the species in this genus are not clear. Although *T. poeyi* has been recorded from central Mexico south to east-central Argentina the validity of many of these records is in doubt. Until recently (Brailovsky, 1983b) South American populations were known under the name *T. bergi.* These populations show some consistent color differences from northern populations and may yet be shown to represent a distinct species. In addition, *T. poeyi* is difficult to separate from *T. striatus*, recorded from central Mexico and Ecuador, on external features. The third species, *T. kormilevi*, is apparently endemic to southern Guatemala.

COMMENTS. The contrasting dark hemelytral veins on a light background allow separation of *Torvochrimnus* species from most other Lygaeinae. *Neacoryphus verecundus* is very similar in general appearance but has a flattened, punctate posterior pronotal lobe.

KEY TO SPECIES OF *TORVOCHRIMNUS* BRAILOVSKY

1. Anterior and middle femora brown dorsally, yellow or ocher ventrally; pronotum with transverse anterior reddish mark; rostral segment I surpassing anterior prosternal margin; bucculae moderately produced 2
—Anterior and middle femora brown except apex ocher; pronotum without transverse anterior reddish mark; rostral segment I scarcely reaching anterior prosternal margin; bucculae slightly produced ..... *kormilevi*
2. Dark maculae to either side of midline on posterior pronotal lobe not reaching callar impressions; blade of clasper about twice as long as shank; length 6.5-6.6mm ..... *striatus*
—Dark maculae to either side of midline on posterior pronotal lobe reaching callar impressions; blade of clasper about as long as shank; length 6.6-8.6mm ..... *poeyi*

PHYLOGENETIC ANALYSIS

The following analysis must be considered provisional. There is not enough information available on the important genitalic characters to allow unequivocal assignment of character state polarity. Also, the analysis does not include the eastern hemisphere representatives of the subfamily. I have used available information on eastern hemisphere genera (mostly from A. Slater, 1985) in making decisions on character state polarity but have not attempted to place those genera phylogenetically.

METHODOLOGY

In general, I have followed the philosophy that taxa should be recognized on the basis of shared apomorphies rather than on all similarities, which would include shared plesiomorphies. The only exception is that I am willing to accept paraphyletic taxa when the paraphyly is based either on ignorance of the true relationships of recognized taxa or on the removal of one or more holophyletic groups showing significant anagenetic distance from those more plesiomorphic taxa united in the remaining paraphyletic unit.

The only taxon recognized here that is not supported as holophyletic by apomorphies is the new genus *Hadrosomus.* The male genitalia of *Biblochrimnus*, the group whose exclusion from *Hadrosomus* might make that genus paraphyletic, were not available for examination. It is quite possible that some of the aedeagal characters found in *Hadrosomus* will be found to be synapomorphies for the genus. Even if this is not the case, I consider the unique structure of the ovipositor of *Biblochrimnus* to provide an important enough suite of characters to justify retention of the two genera.

In constructing the phylogenetic tree (figs. 31-34) I have accepted parsimony as the primary criterion. To choose between multiple equally parsimonious trees, I have relied on my own judgment as to which of the conflicting characters is most likely to reflect the true phylogeny of the group (implicit weighting). Other than this, the only character weighting is that relating to dorsal pubescence (see below), and the implicit weighting of transformation series.

Species were assigned to genera primarily on the basis of uniformity of male and female genitalic structure. Characters used in the analysis were selected because they were consistent within genera and differed between at least some genera. Apomorphies for the entire subfamily, and those uniting species of single genera, though treated in the character analysis where appropriate, were not included in the data set analyzed using PAUP because they contributed nothing to the tree topology.

The genera *Lygaeus* and *Oncopeltus* were not included in the PAUP data set. These are the only lygaeine genera oc-

curring in both Eastern and Western Hemispheres. They are also the only western hemisphere members of a group of genera delimited by the presence of dorsolateral gland openings on the abdominal sterna. This group contains several Old World genera, including some with distinct para- and mediotergites, spermathecal flanges, and basal spermathecal swellings. I consider those character states to be plesiomorphic. If, as I believe, the sternal scent gland openings did not develop more than once, these plesiomorphies indicate that this lineage developed early in the phylogenetic history of the subfamily. *Spilostethus* Stål and *Tropidothorax* Bergroth, the presumed sister genera of *Lygaeus* and *Oncopeltus* respectively, are restricted to the Eastern Hemisphere.

The character set (fig. 28) used to construct the cladogram consisted of 69 characters. Five of these (12, 17, 19, 25, and 43) were treated as unordered for reasons listed in the following character analysis. Three characters (09-11) actually represent a single character coded using mixed ordinal and additive binary coding as described by Pimental and Riggens (1987). Eleven characters (59-69), all concerned with the dorsal pubescence, were assigned weights of 0.5 because dorsal pubescence is known to be highly variable throughout the Lygaeidae.

In assigning direction to the characters used in the analysis I used both the non-lygaeine Lygaeidae and the Pentatomomorpha as a whole as outgroups. This approach was forced by the current lack of knowledge of higher taxon relationships within the Lygaeidae and by the distinct possibility that the family is paraphyletic. In the absence of a well-defined outgroup, acceptance of the most generally distributed state within related higher taxa as plesiomorphic seems to be the best approach. For those characters whose expression in taxa other than the Lygaeinae is poorly documented, I have relied on correlation with better known characters within the subfamily to assign direction.

Characters Not Used in the Analysis

Characters discussed in this section were not used within the character analysis. This was because they were apomorphies for the subfamily as a whole, provided no phylogenetic information for New World taxa alone or were too variable within individual genera to use at this level.

HEAD. The bucculae of most Lygaeidae are low with a straight or slightly convex ventral margin. Such bucculae are also found in those Lygaeinae I consider plesiomorphic on other grounds. I consider this condition plesiomorphic in Lygaeinae. Most Lygaeinae have moderately developed bucculae with a distinctly convex ventral margin while some have extremely well-developed bucculae with very convex ventral margins. I had hoped that this would provide a strong transformation series within the Lygaeinae. Unfortunately, either the bucculae have increased in development several times or there have been many reversions to the plesiomorphic state. Also, there is considerable variation in height and degree of convexity within some genera. For these reasons I have relegated development of the buccula to the generic descriptions instead of including it in the character analysis.

In a few Lygaeinae the bucculae do not extend posteriorly beyond the front of the eye. This characteristic seems to be useful only at the species level.

In some Lygaeinae (and a few non-lygaeine groups) the eyes are borne on distinct stalks. *Nicuesa* is the only western hemisphere genus with stalked eyes, but the character serves to unite *Scopiastes* Stål and its relatives in the Eastern Hemisphere. *Nicuesa* belongs to the group of genera lacking scutellar punctations, while genera in the *Scopiastes* group all possess punctate scutelli. I therefore believe stalked eyes to have developed twice within the Lygaeinae.

PRONOTUM. The greater part of the anterior pronotal lobe of Lygaeinae is taken up by a transverse swelling called the callus. To either side of the midline the callus bears a shiny sinuate groove, the callar impression. The presence of callus and callar impressions may be a synapomorphy of the Lygaeinae as a whole or may be plesiomorphic. Their presence in Lygaeidae seems to be correlated with living on plants rather than on the ground. If ground-living is the plesiomorphic condition in the Lygaeidae, then the callus and its impressions are probably apomorphic; if plant-living is plesiomorphic, then they are probably plesiomorphic.

Schaefer (1975) suggests that plant-living may be the plesiomorphic condition for Lygaeinae. This suggestion is supported by the known habitat of members of genera I consider plesiomorphic, which are, without exception, found on plants. More advanced genera are found on plants, on the ground, or in both habitats. (This does not address the problem of the plesiomorphic lygaeid habitat.) Stys (1967) considers the Cyminae, which live on plants, to be an early offshoot from the main lygaeid line and most other lygaeid subfamilies to be derived from the ground-dwelling Rhyparochrominae. If, as I believe, the Lygaeinae are not derived from the Rhyparochrominae, then there is strong presumptive evidence that plant-dwelling is primitive in the lygaeid lineage. For this reason I do not accept the presence of the callus as an apomorphy for the subfamily.

WINGS. Two major venational terminologies have been used by students of heteropteran wings: that of Comstock and Needham (1898, 1899; modified by Snodgrass, 1935) and that of Leston (1953a), as derived from Tanaka (1926). Recently Hamilton (1972a-c) has proposed a new nomenclature that has not yet been used in studies on Heteroptera. The following discussion uses the terminology of Hamilton. Table 1 shows equivalencies in the three systems as they are applied to the venation of the hind wing.

Table 1. Names for the veins of the heteropteran hind wing. Equivalencies between the terminologies of Hamilton and Comstock and Needham are from Hamilton (1972a,b); between Comstock and Needham and Snodgrass, from Snodgrass (1935); and between Leston and the others, from Leston's later (1962) discussion of his system of homologies and comparison of various figures from the literature where different terminologies were used.

Hamilton	C & N	Snodgrass	Leston
Costa	Costa	Costa	Costa
Subcosta	Subcosta	Subcosta	Subcosta
Radius	$Radius_1$	$Radius_1$	Radius + Media
Sector	Radial sector	Radial sector	Hamus
Media	Media	Media	Cubitus
Cubitus	$Cubitus_1$	$Cubitus_1$	Intervannals
Plical	$Cubitus_2$	$Cubitus_2$	1st Vannal
Empusal	1st Anal	Postcubitus	2nd Vannal
1st Anal	2nd Anal	1st Vannal	Jugal
2nd Anal	3rd Anal	2nd Vannal	———
Jugal Bar	———	———	———

Venation and shape of the costal margin of the corium, useful in the classification of other lygaeid subfamilies, are of no value in the Lygaeinae. The venation is consistent throughout the subfamily and the shape of the costal corial margin varies within genera and often within species.

The lygaeine hind wing is in most aspects like those of other Heteroptera. The main points of phylogenetic interest are the presence at the base of the wing of a distinct subcosta, the single reduced anal vein, and the absence of veins between the branches of the cubital (vannal) fold.

The presence of a distinct subcosta (costa + subcosta of Wooten and Betts, 1986) in the basal part of the wing was considered by Slater and Hurlbutt (1957) to be a plesiomorphic condition in the Lygaeinae. However, judging from the more general studies mentioned above, this characteristic is unique, or nearly so, among the Heteroptera. The only other heteropterans shown to have a distinct subcosta are the Reduviidae and Tingidae (both cimicomorphs), and here the subcosta is distinct from the radius apically rather than basally. While it could be argued that loss of the subcosta or its fusion with other veins has occurred many times, leaving only the Lygaeinae with a basally distinct subcosta, it seems more likely that its presence in this subfamily is apomorphic. I believe this to be one of the stronger synapomorphies uniting the subfamily.

Davis (1961) argues convincingly that the bifid vannal fold of Leston (1953a,b) and of Slater and Hurlbutt (1957) is in fact homologous with the unbranched cubital furrow of Homoptera and other insects and that those authors' jugal fold is the true anal fold. This argument is reinforced by the fact that in Lygaeidae only the so-called jugal vein is associated with the third axillary sclerite, as are the anal veins in other insects. The presence of only a single anal vein is characteristic of most Heteroptera, but because in many lygaeids this vein is well developed, the reduction in the Lygaeinae may be a synapomorphy for the group.

Accepting the presence of only one anal vein in the Lygaeidae, and that it corresponds to the jugal vein in Leston's terminology, the two veins anterior to the anal fold and posterior to the cubital or vannal furrow would presumably be the plical and empusal veins. The two veins within the branches of the vannal or cubital furrow, called intervannals in Leston's terminology, would be the remnants of a branched cubitus and their absence in the Lygaeinae an apomorphic condition.

The hamus, considered by Leston to be "a new vein which has arisen many times," appears to be the remnant of sector as illustrated for *Lethocerus* (Nepomorpha) by Hamilton (1972b, fig. 18). (Though Wooten and Betts, 1986, consider it to be "a relic of the basal section of M," they have apparently ignored Hamilton's work and so their interpretation is doubtful.) Thus its presence in Lygaeinae must be considered plesiomorphic. Its position and degree of development also appear to be plesiomorphic within the Lygaeidae.

Both clavus and corium completely lack punctation in the Lygaeinae. Punctate hemelytra are the norm throughout the Pentatomomorpha. While individual species in many groups lack punctation, the lygaeid subfamily Orsillinae is the only major group except the Lygaeinae in which the majority of species have little or no claval or corial punctation. Even in the Orsillinae there are usually a few punctures on the corium. Because the Orsillinae and Lygaeinae do not seem closely related based on both male and female genitalic characters I consider lack of claval and corial punctation to be a synapomorphy uniting the Lygaeinae.

ABDOMINAL DORSUM. Lygaeinae exhibit scent gland scars between terga IV and V and terga V and VI. This is the most common condition within the Pentatomomorpha. However, many pentatomomorphs both within and outside of the Lygaeidae also have such scars between terga III and IV. The presence of three scars must be considered primitive. Unfortunately, the widespread occurrence of two scars in many groups makes it at best a weak synapomorphy for the Lygaeinae.

Insect spiracular openings on the abdomen are considered to be primitively pleural. In the Lygaeidae they may be either dorsal or ventral. Most authors have considered ventral placement to be the primitive condition because that is the case in the Coreidae, Pyrrhocoridae, and related groups, and because the sublateral impressions on the abdominal venter of many lygaeids were considered to be remnants of pleurosternal sutures. Sweet (1981) has argued convincingly that the so-called outer laterotergites of Lygaeidae are in fact of pleural origin and that consequently the placement of spiracular openings on these sclerites (dorsal) must be considered the plesiomorphic state. His interpretation is supported by Schaefer's (1975) work on trichobothrial ontogeny (see section on trichobothria below) and by my finding, in the course of this study, that the so-called pleural impressions of other Lygaeidae are in fact external indications of tergosternal muscle attachments.

Lygaeinae uniformly have all abdominal spiracular openings on the outer laterotergites. This dorsal placement has long been used as one of the primary features uniting the group. Given Sweet's interpretation, it must be considered a plesiomorphy and cannot be used to define the subfamily.

The terga of several eastern hemisphere lygaeine genera and of the primitive western hemisphere genus *Orsillacis* are divided into three parts by distinct sutures. The outermost two are called paratergites and the inner the mediotergite. Sweet (1981) maintains that such a division of the terga is present in all Lygaeinae. While I have not been able to confirm its presence in all genera studied, a general trend of decreasing sclerotization of the abdominal dorsum within the Lygaeinae makes observation of such structures difficult at best. Those genera in which the dorsum is strongly sclerotized do show the division, and it can be seen in others in which the sclerotization is weaker. I therefore accept the division of the abdominal terga into lateral paratergites and a median mediotergite a synapomorphy for the subfamily.

ABDOMINAL STERNUM. The trichophorous Heteroptera are characterized by the presence of trichobothria on the abdominal venter. Within this group the number, placement, and ontogenetic appearance of these trichobothria may vary both between and within superfamilies. Schaefer (1975) develops a possible phylogenetic interpretation based on detailed study of the variation.

The trichobothrial complement of all adult Lygaeinae examined by me is 3:3:3:3:2 arranged as follows: sterna III and IV each have an irregular transverse row near the midline; trichobothria on sterna V and VI are all lateral, one anterior and two posterior to the spiracle; on sternum VII all are lateral and posterior to the spiracle. This complement and placement is found in most Lygaeidae and is probably the plesiomorphic condition for the family.

Early instar nymphs were unavailable for most species. This lack is especially unfortunate for the genera *Nicuesa*, *Orsillacis*, and *Acroleucus*, which might be expected to show differences in trichobothrial ontogeny if any such variation exists within the subfamily. Those nymphs examined, several species of *Oncopeltus*, *Lygaeus*, and *Ochrimnus*, all displayed the full adult complement in the third instar as was reported for the subfamily by Schaefer (1975). This condition is considered by Schaefer to be more advanced than that in the Plinthisini (Rhyparochrominae), Cyminae, and Blissinae, and less advanced than that in Heterogastrinae and many tribes of Rhyparochrominae. Lygaeid subfamilies similar to the Lygaeinae in trichobothrial ontogeny were the Orsillinae and

Ischnorhynchinae. As Schaefer points out, there is an imperfect correlation between subfamilies with primitive trichobothrial ontogeny and those with dorsal spiracles.

OVIPOSITOR. In most Lygaeidae both valvifers and valvulae are elongate, and the membrane connecting the two halves of each valve is narrow and simple. In many Lygaeinae, however, the valvifers and especially the valvulae are short and the membrane is extensive and highly modified. The generally membranous nature of the ovipositor in Lygaeinae has been considered diagnostic for the group. However, because the character is at best ambiguous and because those Lygaeinae considered here to be more primitive do not display particularly membranous ovipositors, I do not accept it as a synapomorphy for the subfamily.

MALE GENITAL SEGMENTS. In most Lygaeidae abdominal segment VIII is not divided into sternal and tergal sclerites, being at most slightly narrowed dorsally (Ashlock, 1957). In the Lygaeinae, though there are no sutures separating tergum from sternum, there is a distinct area of weakness near each side of the dorsal surface. These areas of weakness seem to delineate a small tergum from a large sternum. If so, their presence in Lygaeinae may be plesiomorphic.

In most Lygaeidae there is no distinct tergum IX, this presumably being either lost or fused with the anterior margin of the opening. In the Lygaeinae, however, there is always a distinct sclerite anterior to segment X, presumably representing tergum IX. This sclerite may be free or partially fused with the anterior margin of the pygophore's dorsal opening. The presence of tergum IX in only the Lygaeinae among Lygaeidae, like the apparent presence of tergum VIII, supports placement of the Lygaeinae as an early offshoot of the lygaeid lineage.

The posterior margin of the dorsal opening of the pygophore often bears a median, anteriorly directed projection, the hypandrium. The development of this projection provides good generic characters in some Old World Lygaeinae (A. Slater, 1985) but does not provide similar characters for New World taxa with the exception of *Hadrosomus*, where it is absent. The lateral margins of the dorsal opening of the pygophore may also bear projections (parandria) and/or sculpturing. Unfortunately, these proved too difficult to examine and interpret to be included in this study. Work on the Australian fauna (A. Slater, 1985) indicates that there may be a correlation between the form of the phallothecal process and the development of the lateral margins of the phallothecal opening. Analysis of the former may serve as the basis for future study of the latter.

CLASPERS. Ashlock (1957) found the base of the shank (the basis parameri) to provide characters in many Lygaeidae. This is not the case in Lygaeinae, where intraspecific variation seems to be as great as interspecific or intergeneric variation. The sculpture of the interior face of the shank, however, provides many good characters within the Lygaeinae.

PHALLUS. Ashlock (1957) notes that the presence of a helicoid process and of phallothecal processes appeared to be mutually exclusive. He thought that the presence of one or the other might be of use phylogenetically in the Lygaeidae. The presence of both in the Lygaeinae may indicate that this is the plesiomorphic state in Lygaeidae or that one or both have arisen more than once.

Sculpture of the phallothecal disc has apparently arisen several times in otherwise not closely related groups. The general form of the sculpture is diagnostic at the genus level and the particulars are also frequently diagnostic at the species level. Unfortunately I have not found it useful above the genus level.

Rugose areas on the disc occur in *Ektyphonotus* and *Oncopeltus* (*Oncopeltus*). As the latter was excluded from the analysis the character was not included in the PAUP data set.

Oxygranulobaphus, *Oncopeltus* (*Erythrischius*), and some eastern hemisphere genera possess a single conical, subapical, dorsal lobe. Because the structure is uncommon I consider its presence apomorphic. However, as *Oxygranulobaphus* is the only genus included in the analysis that displays this character, it was not included in the PAUP data set.

In most, though not all, non-lygaeine Lygaeidae, the vesica is shorter than the conjunctiva. In the Lygaeinae the two are usually, though not always, about equal in length. The vesica is often divided into two roughly equal sections by a heavily sclerotized band, the ring sclerite.

Though very useful in other lygaeid groups, the structure of the ejaculatory reservoir is of little use in the Lygaeinae. The considerable variation in shape is, for the most part, interspecific. A group of eastern hemisphere genera has paired lateral projections arising near the junction of the neck and the seminal duct. In the Western Hemisphere, *Ochrimnus* exhibits an elongated neck and *Achlyosomus* has either a pair of ventrolaterally directed sclerites or pigmented areas on the membrane ventral to the junction of the neck and the seminal duct.

EGGS. Cobben (1968) summarizes information on heteropteran eggs from literature and presents voluminous new information based on his own studies. Unless otherwise mentioned the material presented below is based on that publication.

Cobben's contention that an increase in number of micropyles is apomorphic is supported by the distribution of micropylar numbers in the Pentatomomorpha, where only two or three are found in the Idiostolidae, Thaumastellidae, Rhopalidae (most), and Urostylidae. Within the Lygaeidae the range is 3 to 15. The range within the Lygaeinae is apparently 10 to 14, indicating that this is an advanced feature. I accept presence of 10 or more micropyles as a synapomorphy for the Lygaeinae. However, the presence of 10 micropyles is fairly common throughout the family. Moreover, occasional non-lygaeine species display more than 10, making micropyle number a weak character.

The outwardly directed chorionic micropylar projections, called aero-micropylar processes by Cobben, are typically short and sessile in the Pentatomomorpha, although there appears to be considerable variation within all major subgroups. In the Lygaeidae a majority of Orsillinae have greatly produced and elaborated aero-micropyles, as does the genus *Kleidocerys* of the Ischnorhynchinae.

Within the Lygaeinae most species have short projections. Exceptions are the several eastern hemisphere lygaeinae genera that have elongate, upright aero-micropyles and the western hemisphere genus *Acroleucus*, which has projections of moderate length curved apically in the direction of the center of the cephalic pole. As these structures are not similar in appearance to those of the Orsillinae or of *Kleidocerys*, I do not believe that they represent synapomorphies between the Lygaeinae and either of these taxa. Those lygaeine genera with elongate aero-micropyles are considered by me to be near the base of the lygaeine lineage, and it is possible that elongate aero-micropyles represent a synapomorphy for the subfamily and the short processes in other members a loss. This supposition would be strengthened if the unknown eggs of *Orsillacis* and *Nicuesa* were found to have similar processes. In the absence of this information, and given the uniformity of the gross appearance of the structures in the eastern hemisphere genera and their difference from those of *Acroleucus*, I consider them to be separate apomorphies for each group.

Most lygaeids display a regular polygon at the cephalic pole with as many sides as there are micropyles in the surrounding micropylar ring. The eclosion rupture includes one or more sides of this poly-

gon, and from there continues irregularly away from the pole. The appearance is similar to that of the Piesmatidae, but there the eclosion rupture radiates outward from the angles of the polygon.

The cephalic pole in the Lygaeinae shows an irregular meshwork of many small "cells" within the micropylar circle. This condition is shared by the Cyminae, Artheninae, Blissinae, and Heterogastrinae. The eclosion rupture bisects the pole and continues away from the pole with the ends curving toward each other and becoming irregular near the middle of the egg to form an irregular flap. Since the Idiostolidae also present an irregular meshwork of lines at the cephalic pole and the longitudinal eclosion rupture is considered plesiomorphic within the Heteroptera by Cobben, it seems likely that the lygaeine condition is plesiomorphic rather than representing a synapomorphy with the other subfamilies.

CYTOGENETICS. The microchromosomes (m-chromosomes) are a pair of very small autosomes that often behave differently from other autosomes during meiosis. M-chromosomes are found only within the Heteroptera (Ueshima and Ashlock, 1980), where they are found in most families of Nepomorpha, the Saldidae of the Leptopodomorpha, and within the Pentatomomorpha in most Lygaeidae, Colobathristidae, Hyocephalidae, Stenocephalidae, Rhopalidae, Alydidae, Coreidae, and some Largidae. They are absent in Gerromorpha and Cimicomorpha and in the pentatomomorphan superfamily Pentatomoidea and the families Aradidae, Berytidae, Pyrrhocoridae, some Largidae, and some Lygaeidae.

Ueshima and Ashlock (1980) argue that this distribution within the Heteroptera indicates that the m-chromosomes appeared early in the evolution of the suborder and have been lost several times. Given that the m-chromosomes have not been found outside the Heteroptera, this seems the most logical conclusion. The distribution of taxa with and without m-chromosomes in the trichophorous Pentatomomorpha indicates that presence is the plesiomorphic condition for this group. They are present in the Stenocephalidae, Hyocephalidae, and Rhopalidae, all considered plesiomorphic on other grounds, in the less advanced Largidae, and in the vast majority of Lygaeidae.

Within the Lygaeidae, m-chromosomes are absent in the Lygaeinae, Oxycareninae, and at least two species of Rhyparochrominae (*Targarema stali* B.-White of the Targaremini and *Tropistethus holosericus* (Scholtz) of the Antillocorini). Since the vast majority of the over 140 Rhyparochrominae listed by Ueshima and Ashlock (1980) do have m-chromosomes, their absence in two species is probably not of phylogenetic significance at the subfamily level. Absence in the Lygaeinae and Oxycareninae may be considered either a synapomorphy for the combined subfamilies or as two separate events providing synapomorphies for each individual subfamily. Since I do not consider the Oxycareninae to be closely related to the Lygaeinae on other grounds, I prefer the latter interpretation. Thus the absence of m-chromosomes in Lygaeinae may be considered an apomorphy uniting the group.

Ueshima and Ashlock (1980) show that the most common diploid chromosome complements within the Lygaeidae are 14 (10 macroautosomes, 2 m-chromosomes, and an XY sex mechanism) and 16 (12 macroautosomes, 2 m-chromosomes, and an XY sex mechanism) with a range of 10 to 30. They consider 14 to be the plesiomorphic condition because, in those taxa where both conditions are found, the species with 14 chromosomes are the more primitive on other grounds. Chromosome complements greater than or less than 14 are believed to be derived from that base by fragmentation or combination of chromosomes. This kind of change may be facilitated by the diffuse centromere characteristic of hemipteran chromosomes. The conclusion is supported by the similar macroautosome complements of the Stenocephalidae, Rhopalidae, and Alydidae (Ueshima, 1979) and of the more primitive members of the Largidae (Schaefer, 1964).

Most Lygaeinae have a diploid complement of 14 chromosomes with 12 macroautosomes and an XY sex mechanism. Because the m-chromosomes are absent in Lygaeinae this complement must be considered derived. Unfortunately, the widespread occurrence of species with 12 macroautosomes within the Lygaeidae makes this a weak synapomorphy for the subfamily.

Variation in chromosome number within the Lygaeinae as reported by Ueshima and Ashlock (1980) includes an XXY sex mechanism in *Arocatus suboenus* Montandon, 20 autosomes in *Lygaeus simulus* Distant and *Oncopeltus* (*Oncopeltus*) *famelicus* (Fabricius), and 14 autosomes in *Oncopeltus* (*Erythrischius*) *fasciatus* (Dallas) and *Oncopeltus* (*Oncopeltus*) *nigriceps* (Dallas). As the other *Arocatus* species examined by them has an XY sex mechanism, only the single species of *Lygaeus* and *Oncopeltus* mentioned have 20 autosomes, and as multiple X sex mechanisms and high autosome numbers occur sporadically among the Lygaeidae, it is unlikely that these variations have phylogenetic significance above the species level. The presence of 14 autosomes in representatives of both *Oncopeltus* subgenera indicates that this complement may be a synapomorphy for *Oncopeltus*.

CHARACTER ANALYSIS

The following characters are used in the phylogenetic analysis. Two digit numbers indicate characters and single digit numbers, character states.

01 - Posterior projection of clasper: 0 - thumblike or conical; 1 - absent or reduced to a low bulge. While the shape and degree of development of the projection vary greatly within the Lygaeidae, the majority of illustrations examined seem to show that it is present and at least moderately developed. I have therefore accepted presence of an at least moderately developed projection as plesiomorphic and reduction or absence as apomorphic.

02 - Ventral margin of clasper blade: 0 - smooth; 1 - rugose. The interior (ventral) edge of the blade is smooth in most Lygaeinae. Ashlock (1957) reported at most minute teeth visible only under high magnification in other Lygaeidae.

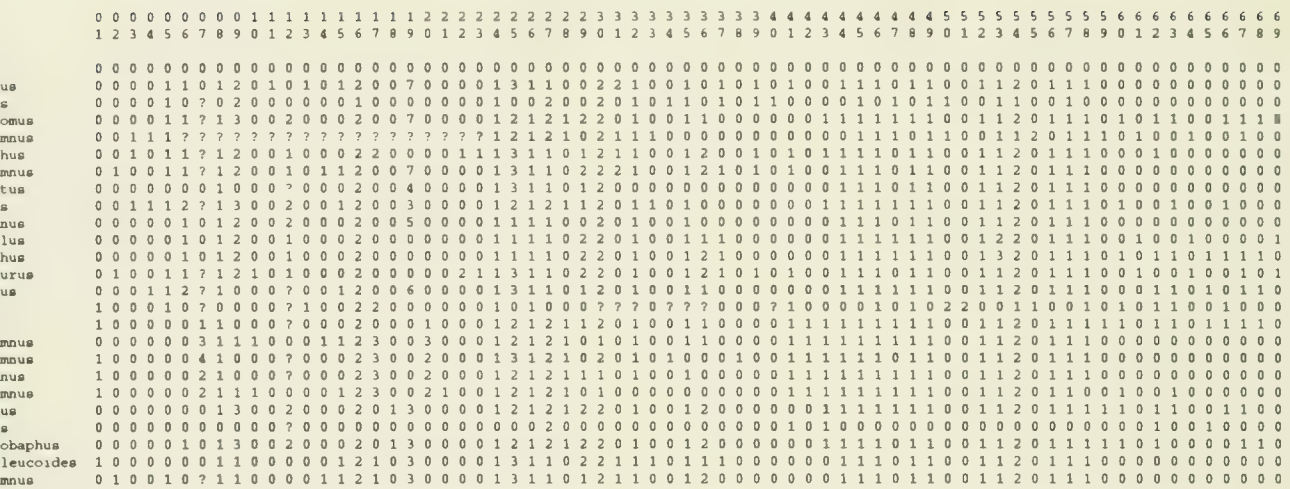
03 - Clasper blade/shank angle: 0 - right or almost right angle; 1 - oblique angle. The blade and shank of most Lygaeinae, and of many if not most Lygaeidae, form roughly a right angle.

04 - Clasper blade thickness: 0 - thick; 1 - thin. The blade is subtriangular and thick in cross section in most Lygaeinae, and in most Lygaeidae. A few lygaeine genera in both hemispheres exhibit a broadened and flattened blade.

05 - Clasper shank median ridge: 0 - present; 1 - absent.

06 - Clasper shank anterior ridge: 0 - absent; 1 - on shank; 2 - on base of blade.

07 - Clasper shank interior projection: 0 - moderately developed, rooflike, projecting laterally; 1 - elongate, projecting somewhat ventrally as well as laterally; 2 - at least 1/2 length of shank, projecting mostly ventrally; 3 - very broad at point of attachment to shank; 4 - point of attachment to shank posterior and vertical. Sculpture on the clasper shank consists of from one to three longitudinal ridges of varying shape and degree of development and a projection near the juncture of shank and blade. The most common condition among Lygaeidae seems to be a modest projection with two ridges. The projection appears to be at the dorsal confluence of the two ridges. The two ridges present in this case would be what I refer to as the posterior and median ridge, as the anterior ridge is never involved with the projection in those species


0 0 0 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 2 2 3 3 3 3 3 3 3 3 3 3 4 4 4 4 4 4 4 4 4 4 5 5 5 5 5 5 5 5 5 5 6 6 6 6 6 6 6 6 6 6
1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9
Ancestor 0 0 0 0 0 0 0 0

western hemisphere genera with the exception of *Orsillacis* and perhaps *Acroleucus*. However, since the genera displaying them are apparently otherwise not closely related, and because the forms that the projections take are so diverse, I consider them to be separately developed. Rather than treat each form as a separate character, I have coded them in a logical progression from absent to sclerotized but treated the character as unordered.

18 - Lateral lobe at base on right side of vesica: 0 - absent; 1 - present. *Ochrostomus* and *Oxygranulobaphus*, possess a single lobe at the base of the vesica. The structure of this lobe, expanded basally and digitiform apically, and their position on the right side of the vesica, are unique to the two genera.

19 - Apical process of secondary gonopore (unordered): 0 - absent or very short, acute; 1 - belled; 2 - swollen with vermiform apex; 3 - moderately elongate, acute; 4 - broad, apex blunt; 5 - broad, apex acute; 6 - extremely elongate, acute; 7 - extremely elongate, almost closed dorsally to form secondary tube. The apical process is an extension of the gonoporal process beyond the secondary gonopore. Ashlock (1957) indicates that it is unique to the Lygaeinae. This agrees well with its distribution within the Lygaeinae where those genera considered more primitive on other grounds lack distinct processes. Process shape is consistent within genera and may vary between genera. Variations in the process consist of either elongation or widening or both. I have been unable to construct a satisfactory transformation series and so treat the character as unordered.

20 - Basal spine placement on vesica: 0 - absent; 1 - present only at apex of digitiform basal lobe; 2 - present at both apex of digitiform basal lobe and in approximately linear series along length of vesica.

21 - Development of basal vesical spine: 0 - short, bases not expanded; 1 - long, bases expanded; 2 - long, bases fused. The basal lobes of the vesica of *Ochrimnus* species are strongly developed and bear stout apical spines as does a single apical lobe. These spine-bearing vesical lobes are unique (with the exception of *Melanopleurus*, see character 22 below) within the Lygaeinae. I have accepted transformation series from no spines to widely distributed for placement and from a relatively small to a relatively large sclerotized area for development.

22 - Enlarged basal lobe on vesica: 0 - absent; 1 - present, conical, unarmed; 2 - present, branched, armed with single spines at apices of branches. *Melanopleurus* is unique among Lygaeinae examined in having apparent paired median lateral conjunctival lobes, bearing apical fields of small spines, as well as elongate spine-bearing vesical lobes. The conjunctiva is much more elongate than in other Lygaeinae, and the elongation apparently occurs distad of the ventral bend of the phallus. This indicates that the apparent median lobes are actually homologous with the subapical lateral lobes of other lygaeines and that the spine-bearing vesical lobes are a uniquely derived feature of *Melanopleurus* rather than an apical displacement of spine-bearing subapical lobes. Given this, and the apparent connection with *Craspeduchus* supported by the shape of the spermatheca and of the phallothecal process, I have accepted a transformation series from no basal vesical lobe through the large conical lobe of *Craspeduchus* to the branched armed lobe of *Melanopleurus*.

23 - Phallothecal process: 0 - not C-shaped; 1 - C-shaped. I have not been able to find a satisfactory transformation series for the various well-developed phallothecal processes. While there are some general similarities between the processes of different genera, only the C-shaped process shared by *Craspeduchus* and *Melanopleurus* is distinctive enough for me to be confident that it provides a synapomorphy.

24 - Spermathecal flange: 0 - present; 1 - absent. In this paper, I accept a spermatheca with a simple tube with globular apical bulb and single flange as plesiomorphic for the Pentatomomorpha because it is apparently the most generally distributed type within the group. Nonetheless, I am not convinced that the presence of a flange or flanges is plesiomorphic. A globular bulb without flanges is found in the Plinthisini (Rhyparochrominae) and in several lygaeine groups. Starting with this formation it is easy to derive all of the more complex spermathecal shapes as providing better leverage for a sperm pumping mechanism.

25 - Apical spermathecal bulb shape (unordered): 0 - spherical; 1 - somewhat elongate; 2 - spindle-shaped; 3 - tubular. Though there are many exceptions, most Pentatomomorpha and Lygaeidae have a globular apical bulb. Those that do not are generally in the relatively more derived taxa of a group. It is not clear that there is a progression from globular to somewhat elongated to spindle-shaped to tubular. I have, therefore, treated apical bulb shape as an unordered character.

26 - Swelling of basal spermathecal tube: 0 - present; 1 - absent. A simple basal tube is present in most Heteroptera, most Pentatomomorpha, and most Lygaeidae. The single notable exception is the Pentatomoidea, in which it is swollen into a saclike structure quite unlike the swellings in Lygaeinae. Because the swelling is strongly correlated with the presence of a globular apical bulb, flange if present, elongate ovipositor, and scutellar punctation, I consider it to be the plesiomorphic condition in Lygaeinae. Its absence in many non-lygaeine Lygaeidae may indicate that it is an apomorphy for the subfamily later lost.

27 - Apical spermathecal tube: 0 - absent; 1 - about as long as basal tube; 2 - much longer than basal tube. The derivation of the sclerotized tubular section of the spermatheca just proximad of the apical bulb is problematic. It may be the result of sclerotization of the apical part of the basal tube or of a narrowing of the base of the bulb. As the apical part of the aedeagal vesica, the secondary gonopore, appears not to penetrate beyond the unsclerotized part of the tube during copulation. It seems that the unsclerotized basal tube and sclerotized apical tube may be separated at least on a functional level, with the unsclerotized tube functioning as a holding mechanism and the sclerotized tube as either a sperm pump or reservoir or both. As those Lygaeinae considered primitive on other grounds lack the sclerotized apical tube I have accepted increasing tube length as apomorphic. This structure occurs elsewhere in the Lygaeidae (e.g., Orsillinae), and is found in both Old and New World lygaeine genera. Thus it appears that it has arisen several times.

28 - Basal pockets on ovipositor membrane: 0 - absent; 1 - present. In most Lygaeinae the genital chamber is defined by a simple membrane. Those lygaeine genera with conjunctival (*Ochrostomus* and its allies) or vesical (*Ochrimnus*) spines in the males display pockets in the ventral membrane of females. These pockets are either greatly thickened membrane or possibly lined with sclerotized material. The pockets are irregularly shaped and may conform somewhat to the shape of the spines that they receive during copulation. I have found no mention in literature of similar pockets in other Lygaeidae with aedeagal spines. Thus their presence in Lygaeinae appears to be apomorphic.

29 - Y-sclerite of first ovipositor valve: 0 - absent; 1 - not reaching apex of membrane; 2 - surrounding apex of membrane. The middle of the membrane of the first ovipositor valve frequently bears a longitudinal sclerite. In many species this sclerite splits at the base of the cleft and continues along the margins of the cleft for a varying distance. I have not seen such a sclerite in other Lygaeidae, and it may be that its presence is an apomorphy for the Lygaeinae. However, some Lygaeinae, especially in the more plesiomorphic groups, lack the sclerite. I have established a transformation series for this character ranging from absent, to present but not reaching the apex of the membrane, to extending around the apex of the membrane. As the function of this sclerite seems to be to

stiffen the membrane during oviposition, the outlined progression seems functionally sound.

30 - Apical extension of first ovipositor valve membrane: 0 - not surpassing apex of valvula; 1 - surpassing apex of valvula by less than 1/5 length of valvula; 2 - surpassing apex of valvula by at least 1/3 length of valvula. Most Lygaeidae display no great development of the first ovipositor valve membrane beyond the apex of the first valvulae. In many Lygaeinae the valvulae are very short and part of their function of guiding eggs during oviposition has been assumed by the membrane. The membrane in these species extends greatly beyond the apex of the valvulae, often by the length of the valvulae. I have somewhat arbitrarily divided the Lygaeinae into two groups, a plesiomorphic group in which the membrane extends beyond the apex of the valvula by less than 1/5 the valvular length and an apomorphic group where it extends beyond the valvula by at least 1/3 the valvular length. These groupings correlate well with other characters although scattered genera within the apomorphic group - *Ochrimnus* (*Phaeochrimnus*), for example - display the plesiomorphic condition.

31 - Lateral cleft of first ovipositor valve membrane (unordered): 0 - absent; 1 - lateral projection short; 2 - lateral projection long. Some Lygaeinae exhibit a secondary cleft between the median cleft and the valvula, resulting in two projections of the membrane apically at either side of the cleft. I have not found a similar development mentioned in literature on other Lygaeidae or Pentatomorpha. In some genera this projection is quite short, not reaching the apex of the valvula, while in others it is more elongate and greatly exceeds the apex of the valvula. I have accepted a transformation series for this structure from no projection through a short projection to a long projection.

32 - Median cleft of first ovipositor valve membrane: 0 - reaching less than 1/5 distance to base of valvula; 1 - reaching at least 1/3 distance to base of valvula. The connecting membrane of the first valve in all lygaeids for which I have been able to find illustrations has at least a small median cleft. In many lygaeines this cleft extends almost to the level of the base of the valvula. As this cleft is very shallow in most Lygaeidae and in those Lygaeinae considered plesiomorphic on other grounds, I consider the deep cleft the apomorphic condition. Though the depth of the cleft varies considerably, I have not been able to derive a satisfactory transformation series based on this variation and so have arbitrarily split the subfamily into two groups based on the largest gap in extent of the cleft.

33 - Lateral sclerite of first ovipositor valve membrane: 0 - absent; 1 - present. In addition to the median or Y-sclerite, the membrane may bear a sclerotized area in the membrane between the median cleft and the valvula. I have been unable to find any mention of such a sclerite outside the Lygaeinae.

34 - Projection at base of median cleft of first ovipositor valve membrane: 0 - absent; 1 - present. Acroleucus and *Ochrimnus* (*Orthochrimnus*) have a bluntly rounded median projection at the base of the median cleft of the membrane. I have not found such a projection elsewhere in Lygaeidae.

35 - Median cleft of second ovipositor valve membrane: 0 - extending less than 1/5 distance to base of valvula; 1 - extending at least 1/3 distance to base of valvula.

36 - Lateral margin of second ovipositor valve membrane median cleft: 0 - without shoulder or projection; 1 - interrupted by distinct shoulder or blunt projection; 2 - acute projection. The connecting membrane of the second ovipositor valve is never so extensively developed as that of the first. The membrane projects at most slightly beyond the apex of the valvula. I have coded the extent of the median cleft as I did the median cleft of the first valve. In some genera there are apical projections at the lateral margins of the median cleft. As most Lygaeidae do not have such projections, I have accepted a transformation series from no projection to a slight projection to an acute projection. There seems to be no correlation between presence or development of these projections and presence or development of the lateral projections of the membrane of the first valve.

37 - Lateral sclerite of second ovipositor valve: 0 - absent; 1 - present. There is rarely a distinct Y-sclerite as in the first valve, but in some genera the margins of the median cleft are strongly pigmented or sclerotized. Only a few of the genera exhibiting a well-developed Y-sclerite on the first valve show this development. It seems to be roughly correlated with the presence of a large, laterally directed, subapical lobe on the conjunctiva of the aedeagus.

38 - Ovipositor second valve median projection at base of cleft: 0 - absent; 1 - present. As with the first valve, both *Acroleucus* and *Ochrimnus* (*Orthochrimnus*) display a blunt median projection at the base of the median cleft of the connecting membrane.

39 - Median swelling of second valvula dorsal margin: 0 - absent; 1 - present. Craspeduchus, Melanopleurus, Dalmochrimnus, and *Achlyosomus* display a very distinct elongate bulge along the dorsal margin of the second valvula. There is some variation in placement among genera, but it is always at least near the middle of the margin. The most similar feature found among other Lygaeinae is a subapical bulge, found in many other genera.

40 - Callus interrupted medially: 0 - no; 1 - yes. The callus forms a complete ridge across the pronotum in all Lygaeinae except *Acroleucus*, where it is broken on each side of the midline by a depression connecting depressed areas in front of and behind the callus, and in the genera *Nicuesa* and *Oncopeltus* (both subgenera), where the callus is so low as not to be well differentiated from the rest of the pronotum. As the callar impressions are well developed in all of these genera, I consider the incomplete, or obsolete, callus to be apomorphic. Because the callus is obsolete in *Nicuesa*, it is not possible to determine whether it would have been interrupted medially as in the closely related *Acroleucus*. Thus the placement of this character on the tree is uncertain. It could be a synapomorphy either uniting the two genera or the members of *Acroleucus* alone.

41 - Postcallar impression interrupted laterally: 0 - no; 1 - yes. Behind the callus is a transverse impression that separates the anterior and posterior pronotal lobes. In most Lygaeidae this depression is uninterrupted, and I consider that the plesiomorphic condition.

42 - Postcallar slits: 0 - absent; 1 - present. All subgenera of *Ochrimnus* have a transverse series of four slits in the postcallar impression. Other genera usually have punctures of varying depth in that area but nothing approaching a distinct series of slits.

43 - Callar impression (unordered): 0 - unbranched; 1 - branched. The callar impressions are either unbranched or have a short posterior arm at their median ends. I am unable to argue convincingly that either state is plesiomorphic. While the impressions of most otherwise plesiomorphic genera lack branches, in the genus *Orsillacis* the branches are very distinct. Therefore, I have treated this character as unordered. The form is constant within genera but either the branch has developed many times or been lost many times within the subfamily.

44 - Eye placement: 0 - sessile but distinctly separated from pronotum; 1 - adjacent to pronotum. In many non-lygaeine Lygaeidae the eyes, while sessile, are distinctly separated from the anterior angles of the pronotum. I consider this to be plesiomorphic. In most Lygaeinae (and some non-lygaeine groups) the eyes are contiguous with the anterior pronotal angles. I consider this a strong synapomorphy for those lygaeine genera possessing the feature.

45 - Hemelytral membrane: 0 - translucent; 1 - opaque. The membranous apical part of the hemelytron is transparent or translucent in the majority of Pentatomomorpha and especially within

the Lygaeidae. Within the Lygaeinae those genera with punctate scutelli, and the Western Hemisphere genera *Acroleucus* and *Nicuesa*, which lack scutellar punctation, have a translucent membrane. In the rest of the genera the membrane is opaque.

46 - Scutellar punctations: 0 - present; 1 - absent. The scutellum of most Lygaeidae is strongly punctate. I consider the presence of punctation to be the plesiomorphic condition for Lygaeinae.

47 - Shape of posterior metapleural margin dorsad of acetabula: 0 - straight or slightly concave; 1 - convex. The posterior margin of the metapleuron may be either straight, concave, or convex. As a straight, or almost straight, margin appears to be the most generally distributed condition in Lygaeidae, I accept this as the plesiomorphic state. A concave margin may be the result of either posterior development of the dorsal part of the pleuron (not exhibited by Western Hemisphere Lygaeinae) or of the acetabula (character 55). A convex margin is the result of posterior development of the middle of the posterior pleural margin. This appears to have occurred more than once in the Western Hemisphere.

48 - Metapleural punctation: 0 - distinct; 1 - absent. Most Lygaeidae have very strongly punctate thoracic pleura. I consider this the plesiomorphic condition. In Lygaeinae there appears to be a trend toward reduction in extent and depth of this punctation. On the pro- and mesopleura this trend is gradual, with numerous taxa showing very faint punctures. Due to the difficulty of deciding which taxa are completely impunctate I have not used the punctation of these pleura in my analysis. The punctation of the metapleuron, on the other hand, is clearly either present or absent.

49 - Metapleural ostiolar peritreme apex: 0 - distinctly separated from metapleuron anteriorly, posteriorly and dorsally; 1 - distinctly separated from metapleuron posteriorly and dorsally. The apex of the peritreme consists of a rounded, raised area made distinct from its surroundings by its velvety appearance. In those Lygaeinae with extensive evaporative areas (character 54), this area is distinctly separated from the surrounding pleuron by a short or long stalk. In most other Lygaeinae the anterior margin merges with the surrounding pleuron, while the dorsal and posterior margins are separated by a groove which I believe is the remnant of the stalk.

The correlation between well-developed peritreme and large evaporative area is the reverse of that found by Schaefer (1972) in a review of the trichophorus Heteroptera. Slater (1979) illustrates what he considers to be the plesiomorphic peritreme in Blissinae, which bears a striking resemblance to the most common state within the Lygaeinae. Nonetheless, I have accepted the moderately stalked peritreme and extensive evaporative area as plesiomorphic for the Lygaeinae.

50 - Height of metapleural margin anterior to peritreme: 0 - much higher than posterior margin; 1 - slightly higher than posterior margin; 2 - as high as posterior margin. In most Lygaeidae the channel leading from the ventral opening of the metathoracic scent gland to the velvety apex of the peritreme is roofed laterally by its anterior margin, thus directing the opening at least slightly to the rear. This anterior margin is usually distinctly higher than the adjacent posterior margin. In *Acroleucus* the anterior margin is only slightly higher than the posterior, and in *Nicuesa* they are about the same height. Since these are the only lygaeines in which this occurs, I have accepted the reduction in height as apomorphic.

51 - Flattened area of metapleural margin anterior to peritreme 1: 0 - narrow but distinct; 1 - broader; 2 - still broader.

52 - Flattened area of metapleural margin anterior to peritreme 2: 0 - narrow but distinct; 1 - absent. The breadth of the metapleuron anterior to the scent gland channel varies greatly in Lygaeidae. In the Lygaeinae, *Orsillacis* and other genera with punctate scutelli have a narrow but distinct flattened area. *Acroleucus* and *Nicuesa* have a broad flattened area, that of *Nicuesa* much the broadest. The rest of the genera have no flattened area but rather have a low ridge immediately anterior to the upward-flaring margin of the channel. As I consider those genera with punctate scutelli to be plesiomorphic I have accepted both broader and absent states as apomorphic.

53 - Shape of metapleural ostiolar peritreme apex: 0 - rounded; 1 - slightly elongate dorsally; 2 - extremely elongate dorsally. The shape of the velvety area differs slightly between, and sometimes within, genera but is usually roughly circular. In *Lygaeospilus* it is distinctly ovate with the long axis oriented dorsoventrally and in *Melacoryphus* it is even more elongate.

54 - Metapleural evaporative area: 0 - broadly surrounding apex of peritreme, extending onto mesopleuron as far as acetabular cleft; 1 - broadly surrounding apex of peritreme, extending onto mesopleuron only along posterior margin; 2 - narrowly surrounding apex of peritreme, not extending onto mesopleuron. The evaporative area is very extensive in most Lygaeidae. *Orsillacis* and other lygaeine genera with punctate scutelli have the largest evaporative areas, extending onto the mesopleuron as far as the acetabular cleft. In *Acroleucus* and *Nicuesa* the evaporative area is less extensive, reaching only the posterior margin of the mesopleuron, but still covering about a third of the metapleuron. In other members of the subfamily the area is much reduced, being restricted to the margins of the peritreme channel and a very narrow band around the apex of the peritreme.

55 - Metapleural acetabula enlarged: 0 - at most 1/2 length of rest of posterior metapleural margin; 1 - about length of rest of posterior metapleural margin. As mentioned above (character 47) a straight or nearly straight posterior metapleural margin is most generally distributed throughout the Lygaeidea. In some Lygaeinae this margin appears concave due to an increase in the size of the acetabula.

56 - Metapleural acetabula reduced: 0 - at least 1/2 length of rest of posterior metapleural margin; 1 - about 1/3 length of rest of posterior metapleural margin. Reduction in extent of the acetabula does not appear to affect the shape of the posterior margin. The directionality of this character is not well supported. As the eastern hemisphere genera with punctate scutelli have acetabulae similar to that of *Orsillacis*, I have simply accepted the structure exhibited by *Orsillacis* and those other genera as plesiomorphic.

57 - Abdominal sterna II and III fused: 0 - no; 1 - yes. In most Lygaeidae, sterna II through V of males and II through IV of females are fused. In the Lygaeinae, females of *Orsillacis*, *Acroleucus*, and *Nicuesa* in the Western Hemisphere and *Caenocoris* in the Eastern Hemisphere show no sternal fusion. Males of these genera have reduced but visible intersegmental conjunctivae between III/IV and IV/V. The eastern hemisphere genus *Thunbergia* has reduced but visible conjunctivae between III/IV in females and between III/IV and IV/V in males. Members of the primitive rhyparochromine tribe Plinthisini are the only other lygaeids known to me to lack sternal fusion. I therefore consider this lack of fusion to be a primitive condition in the Lygaeinae as well as in Lygaeidae as a whole. Accepting the Lygaeinae as a holophyletic group, the fusion of these sterna becomes an apomorphic feature, though it appears that it has happened at least twice, once within the group of genera possessing punctate scutelli and once within the group of genera lacking scutellar punctures.

58 - Abdominal sternum VI much shortest medially: 0 - yes; 1 - no. The elongate ovipositor of most Lygaeidae often, but not always, accompanies modification of abdominal sterna VI and VII. In VI this modification generally takes the form of a reduction in median length rather than a distinct cleft. The longer the ovipositor the greater is this reduction. In those Lygaeinae exhibiting many plesiomorphic character states, the ovipositor tends, with some no-

table exceptions, to be more elongate than in those exhibiting many apomorphic character states. The median length of segment VI reflects this. I have, somewhat arbitrarily, chosen to consider a median length of greater than 1/2 the lateral length as the apomorphic condition. This correlates well with other characters.

59 - Density of predominant cephalic hairs: 0 - dense; 1 - sparse.
60 - Length of predominant cephalic hairs: 0 - moderate; 1 - very short.
61 - Long, upright cephalic hairs: 0 - absent; 1 - present.
62 - Density of predominant pronotal hairs: 0 - dense; 1 - sparse.
63 - Length of predominant pronotal hairs: 0 - moderate; 1 - very short.
64 - Long, upright pronotal hairs: 0 - absent; 1 - present.
65 - Density of predominant scutellar hairs: 0 - dense; 1 - sparse.
66 - Length of predominant scutellar hairs: 0 - moderate; 1 - very short.
67 - Density of predominant hemelytral hairs: 0 - dense; 1 - sparse.
68 - Length of predominant hemelytral hairs: 0 - moderate; 1 - very short.
69 - Long, upright hemelytral hairs: 0 - absent; 1 - present.

Within the Lygaeinae there is variation in length and density of dorsal pubescence on the head, pronotum, scutellum, and hemelytra. As both types of variation may occur independently on one or all of these structures, I have treated each as a separate character. Both hair length and density are so variable within the Lygaeidae as a whole that these characters were given weights of 0.5 in the analysis.

Though it varies considerably, the dorsal pubescence of most Pentatomomorpha, and Lygaeidae, consists of scattered, very short, appressed hairs. In contrast, the dorsal surface of most western hemisphere, and many eastern hemisphere, Lygaeinae is moderately densely clothed with short, semi-decumbent hairs. Because this type of pubescence is found in those lygaeine genera with scutellar punctation and elongate ovipositors, I consider it to be the plesiomorphic condition in Lygaeinae.

Some Lygaeinae have on the dorsum a number of long upright hairs of about the same thickness as the rest of the dorsal pubescence. As this is an uncommon trait throughout the Lygaeidae, I consider it to be apomorphic.

The most common variation is reduction in length, either with or without decrease in density. Because it has apparently occurred many times, this must be considered a weak character. It seems most useful in providing a synapomorphy uniting the species of several genera.

RELATIONSHIPS

Possible synapomorphies uniting the subfamily are: ocular microtrichia of first instar larvae absent; forewing without claval or corial punctation; subcosta of hind wing distinct basally; hind wing with only one anal vein; hind wing without intervannals; abdominal dorsum divided into paratergites and mediotergites; egg with at least 10 micropyles; m-chromosomes absent; base number of macroautosomes 12. Of these I consider the absence of punctures on the forewing, presence of a distinct basal subcosta on the hind wing, and lack of m-chromosomes to provide the strongest evidence for the hypothesis that the Lygaeinae comprise a holophyletic group.

Analysis of relationships within the subfamily is based on a PAUP analysis rooted on the presumed ancestor - defined as having state 0 for all characters. The analysis produced 30 equally parsimonious trees with length 194.5 and a consistency index of 0.476. The strict consensus tree based on these 30 trees (fig. 29) shows *Orsillacis* as the sister group of all the remaining genera and a group containing *Acroleucus* and *Nicuesa* as the sister group of all the genera except *Orsillacis*.

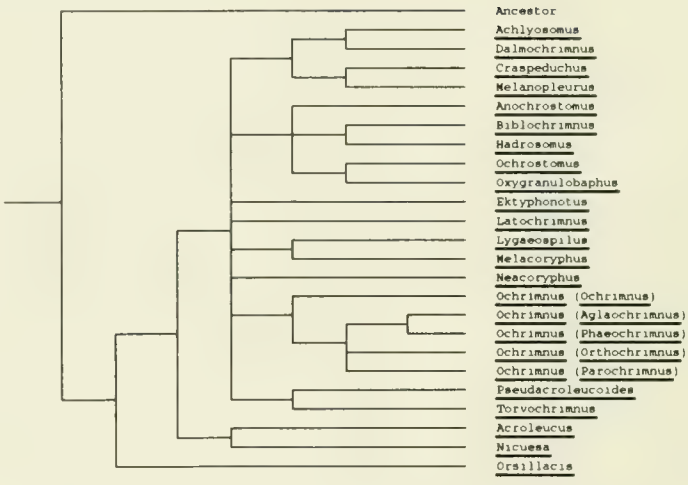


Fig. 29. Strict consensus tree based on 30 equally parsimonious trees produced by analysis using PAUP v.2.4.1.

Comparison of the 30 trees shows that they can be divided into two roughly equal groups. One group, consisting of 14 trees, shows *Ochrimnus* as the sister group of all genera except *Orsillacis* and *Acroleucus* plus *Nicuesa*. The other group, consisting of 16 trees, shows *Ektyphonotus* as the sister group of all except those three genera and *Ochrimnus* as the sister group of *Ochrostomus* and allied genera. Because I consider the unique shape of the spermatheca (ch. 25, state 2) and presence of basal pockets in the membrane of the ovipositor (ch. 28, state 1) common to *Ochrimnus* and the group containing *Ochrostomus* to be very strong apomorphies, the 14 trees with *Ochrimnus* as the sister group of most genera were rejected. Reanalysis with character 28 weighted as 100 to force *Ochrimnus* and the *Ochrostomus* group together produced the same 16 trees exhibiting this feature as the original analysis.

The consensus tree for the 16 remaining trees (fig. 30) shows only four multifurcations, each of them a trifurcation. These trifurcations are the result of two possible placements each of the group *Torvochrimnus* plus *Pseudacroleucoides*, the genus *Latochrimnus*, the genus *Anochrostomus*, and the *Ochrimnus* subgenera *Orthochrimnus* and *Parochrimnus*. These placements will be discussed below.

The proposed phylogenetic tree (figs. 31-34) differs from this consensus tree only in the resolution of the trifurcation within *Ochrimnus*.

The single species of *Orsillacis* is most similar in general appearance to some Old World genera. The basal swelling of the spermatheca is very similar in appearance to that of the Old World genera *Scopiastes* and *Scopiastella* and may be an apomorphy for the three genera.

It is tempting to recognize *Orsillacis* and the Old World genera with punctate scutelli as a distinct tribe. This would correspond to the Arocataires of Mulsant and Rey (1878). At present, however, they are united solely on the basis of

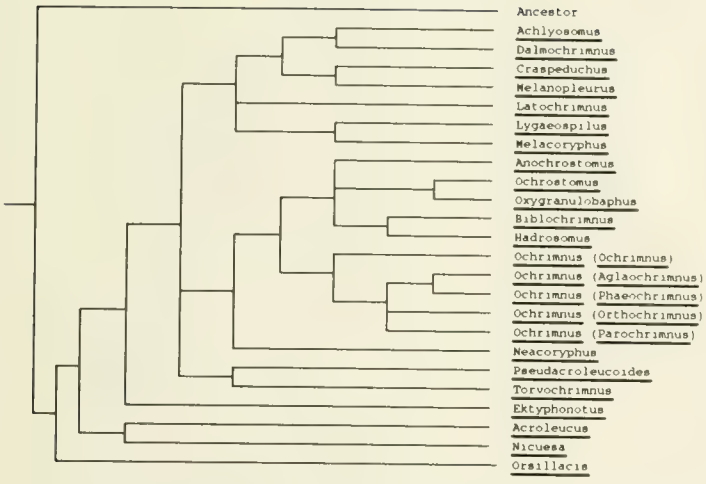


Fig. 30. Consensus tree based on 16 equally parsimonious trees with *Ochrimnus* and the *Ochrostomus* group as sister groups.

plesiomorphies. A possible synapomorphy for such a group is greatly elongate aero-micropylar projections of the egg. Unfortunately the egg is unknown for most species including the single *Orsillacis* species. Another possible synapomorphy is the presence of a spermathecal flange. As mentioned in the character analysis, I have treated presence as the plesiomorphic condition but have some reservations about this.

It is possible that interruption of the pronotal callus, treated here as a synapomorphy for *Acroleucus*, should be treated as a synapomorphy for the group *Acroleucus* plus *Nicuesa*. Because the callus is obsolete in *Nicuesa*, this cannot be verified. A further possible synapomorphy is the reduction in length and increase in width of the ovipositor, most strongly displayed in the mostly membranous ovipositor of *Nicuesa*. Some species of *Acroleucus* have a flat interior projection of the first valvula which could easily be considered a precursor to the platelike first valvula of *Nicuesa*. This fact could be taken as indicating that *Acroleucus* is paraphyletic, but the unique spermatheca and sclerotized subapical conjunctival lobe common to all species of *Acroleucus* and the more primitive spermathecal type and lack of conjunctival lobe of *Nicuesa* argue against such an interpretation.

The group consisting of all genera except *Orsillacis*, *Acroleucus*, and *Nicuesa* is the one most strongly supported by the characters used in the analysis. I consider characters 44, 45, 49, 54 and 57 to be most important. This group would probably also contain all Old World genera except those allied to *Orsillacis*, although it is quite possible that the group of Old World genera bearing anterolateral gland openings on the abdominal sterna would split off somewhere within the internode.

The placement of *Ektyphonotus* on the tree is very weakly supported, as the internodes separating it from the remaining genera contain only five characters with a maximum consistency of 0.375.

Two equally parsimonious placements on the tree of the group *Torvochrimnus* plus *Pseudacroleucoides* are possible. It may be either the sister group of all other genera beyond *Ektyphonotus* (Groups 1 and 2 of fig. 31) or of *Melacoryphus* and allies (Group 1 only). Because the characters supporting either placement of the group are weak, I have left the trifurcation unresolved.

Though *Neacoryphus* is placed as the sister group of those genera with pockets in the basal membrane of the ovipositor (Group 2 of fig. 31) on all 16 trees, its position is weakly supported. It is placed only on the basis of the convex posterior margin of the metapleuron. This character is very weak, with a consistency index of 0.2. In general appearance the two species of the genus are quite similar to *Melacoryphus*. In fact, until recently (A. Slater, 1988) all members of *Melacoryphus* were included in *Neacoryphus*. It is primarily lack of some features present in *Melacoryphus* and its allies that eliminates *Neacoryphus* from that group.

Given the uncertain placement of the genera *Ektyphonotus* and *Neacoryphus*, and of the group *Torvochrimnus* plus *Pseudacroleucoides*, it is tempting to consider the remainder of the genera as forming a holophyletic group. With the exception of *Ochrimnus* these genera all have highly developed sublateral conjunctival lobes bearing spines. (The eastern hemisphere genera *Achrobrachys*, *Caenocoris*, and *Thunbergia* also have well developed conjunctival lobes, but those genera belong to the group with scutellar punctations and the development of the lobes is quite dissimilar.) Many have a short anterior ridge and lack a median ridge on the shank of the clasper. Because the development of the lobes differs significantly between *Melacoryphus* and its allies on one hand and *Ochrostomus* and its allies on the other, and because, as mentioned above, I consider *Ochrimnus* to be closely related to the *Ochrostomus* group, I have not united them on the tree.

The shape of *Latochrimnus* apical spermathecal bulb (ch. 25) places it as the sister group of *Lygaeospilus* and *Melacoryphus*. The armature of the subapical conjunctival lobes (ch. 12) and absence of a Y-sclerite (ch. 29) place it as the sister group of that group plus *Craspeduchus* and allies. Because the opposing placements seem to me to be about equally likely I have left the trifurction unresolved.

Despite the few characters supporting it, the group *Melacoryphus* plus *Lygaeospilus* appears in all of the trees. It is supported most strongly by the dorsoventral elongation of the apical button of the ostiolar peritreme (ch. 53, state 1). This condition is also found in *Lygaeus*, *Oncopeltus*, and presumably related Old World genera. Should my hypothesis that *Lygaeus* and *Oncopeltus* belong to a lineage branching early on the lygaeine tree be proved false, this might indicate a close relationship between the two groups.

The remaining major group consists of *Ochrimnus* plus *Ochrostomus* and its allies. This group is most strongly supported by the unique spermatheca shape (ch. 25, state 2) and by the presence of pockets in the membrane at the base of the ovipositor (ch. 28). If, as seems possible, the characteristic spine-bearing vesical lobes of *Ochrimnus* are derived

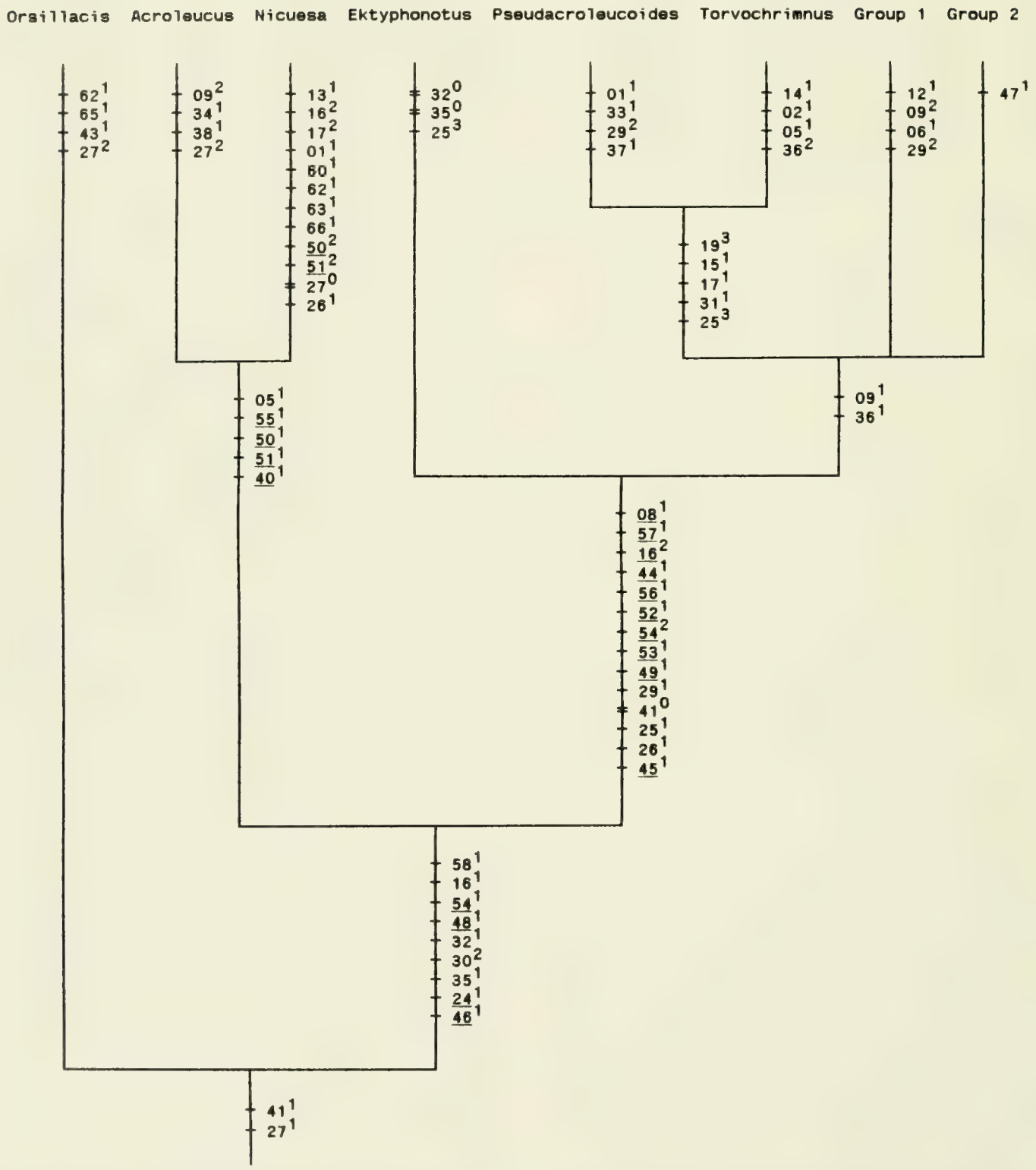


Fig. 31. Character distributions at base of proposed phylogenetic tree. Underlined characters have a consistency index of 1.00. Changes to a more derived state are indicated by a single crossbar, those to a less derived state by a double crossbar. Superscripts indicate the character state. Group 1 = *Melacoryphus* A. Slater and allies. Group 2 = *Ochrimnus* Stål and allies.

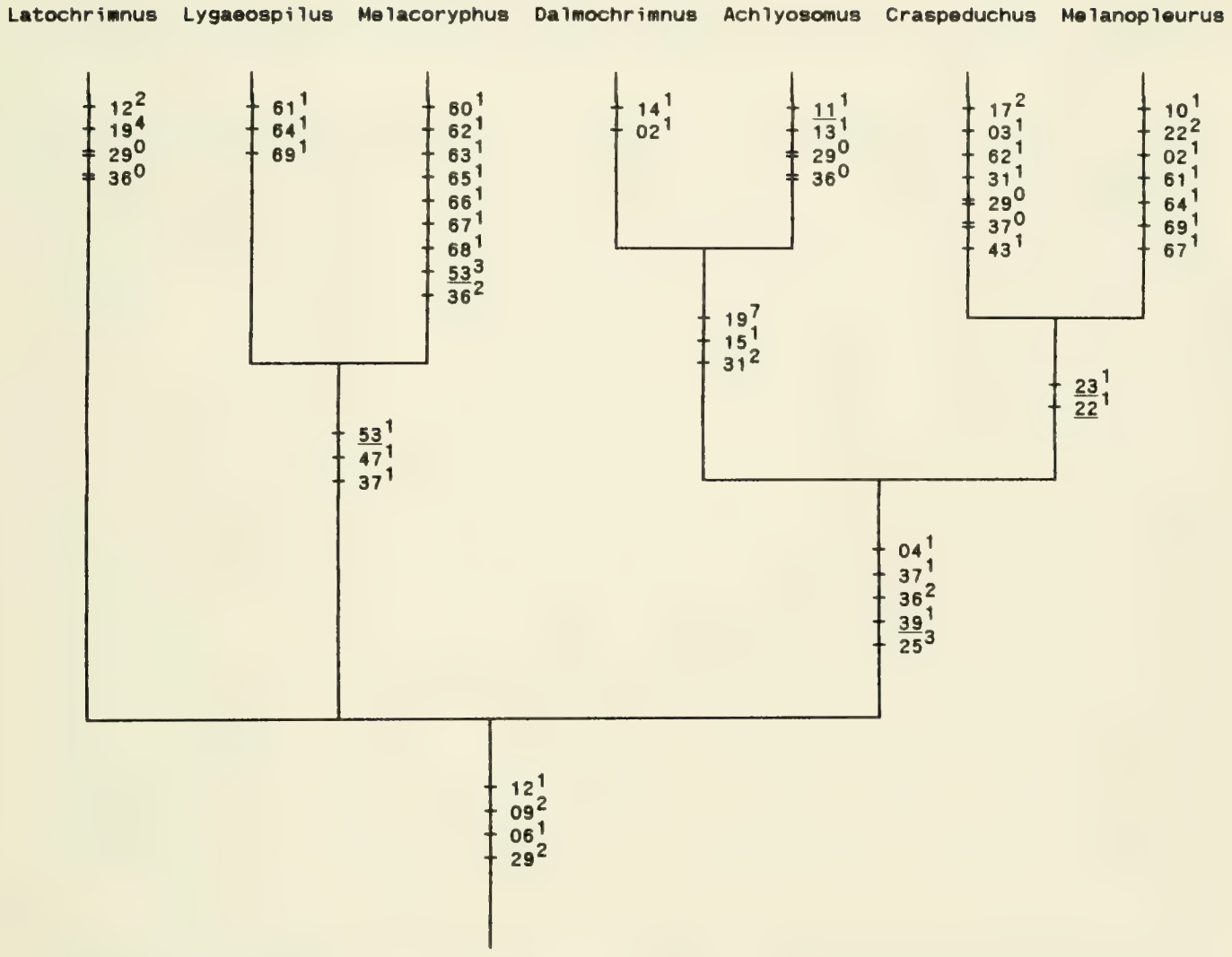


Fig. 32. Character distributions for *Melacoryphus* A. Slater and allies. Underlined characters have a consistency index of 1.00. Changes to a more derived state are indicated by a single crossbar, those to a less derived state by a double crossbar. Superscripts indicate the character state.

from the spine-bearing conjunctival lobes of the *Ochrostomus* group, that transformation series would add additional strength to the grouping.

The position of *Anochrostomus* is unclear. The major character uniting the genus with *Ochrostomus* plus *Oxygranulobaphus* is the extension of the Y-sclerite of the first ovipositor valve to surround the apex of the membrane (ch. 29, state 2). This extension occurs in other groups. The remaining characters (ch. 62, 67) pertain to the dorsal pubescence. The lack of a median ridge on the shank of the clasper (ch. 05) supports placement of the genus with the group *Hadrosomus* plus *Biblochrimnus*. Because both characters are subject to homoplasy, I have left the placement of *Anochrostomus* as an unresolved trifurcation.

My preferred tree (fig. 34) shows the branch bearing *Ochrimnus* (*Parochrimnus*) as basal to that bearing *Ochrimnus* (*Orthochrimnus*), while the consensus tree (fig. 30) shows them as part of a trifurcation. This results from conflicting distributions of characters 29 (the development of the Y-sclerite) and 30 (the apical development of the membrane). The presence of a Y-sclerite is apparently unique to Lygaeinae. The character has a low consistency (0.2) in part due to apparent losses of the sclerite and in part due to an apparent tendency for it to increase in length towards the apex of the membrane. The Y-sclerite in *Ochrimnus* (*Parochrimnus*), while present, is reduced from that in *Ochrimnus* (*Ochrimnus*). It is absent in the remaining subgenera. The distribution of character 30, the character suggesting that *Ochrimnus* (*Orthochrimnus*) should branch first, may be equally parsimoniously explained with *Ochrimnus* (*Parochrimnus*) branching first, the former requiring a reversal and a re-reversal, the latter two separate reversals in the same di-

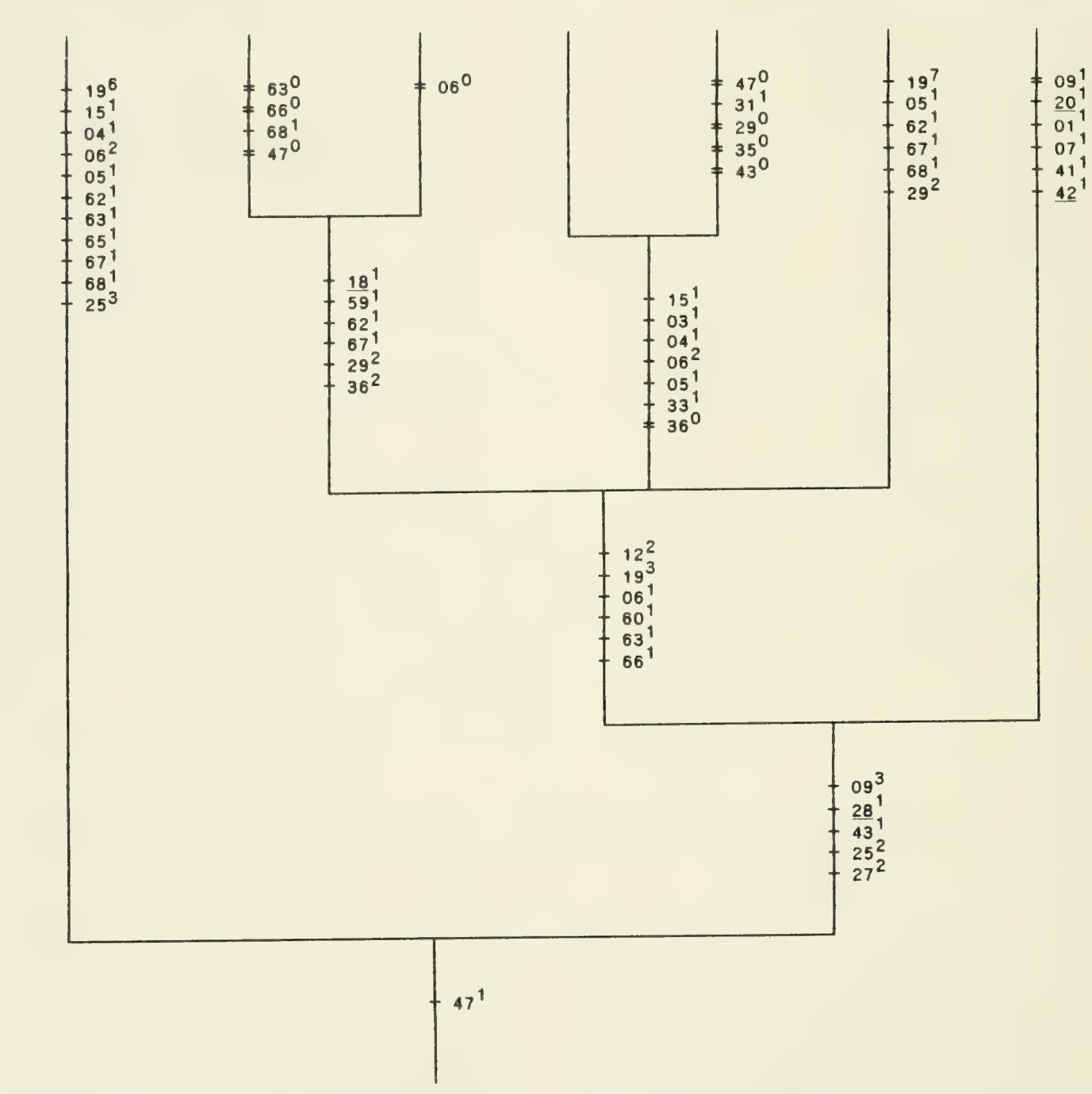


Fig. 33. Character distributions for *Ochrimnus* Stål and allies. Underlined characters have a consistency index of 1.00. Changes to a more derived state are indicated by a single crossbar, those to a less derived state by a double crossbar. Superscripts indicate the character state.

rection. I therefore prefer to rely upon the evidence of the Y-sclerite and resolve the trifurcation.

The holophyly of *Ochrimnus* (*Parochrimnus*) is supported most strongly by the presence of many spines forming a longitudinal series on the base of the vesica. Species were assigned to the subgenus primarily on the basis of this characteristic. Since I was unable to obtain complete inflations of the aedeagus for all species it is possible that some species are incorrectly assigned to the subgenus. Thus the character distribution for the subgenus is in doubt and it may well

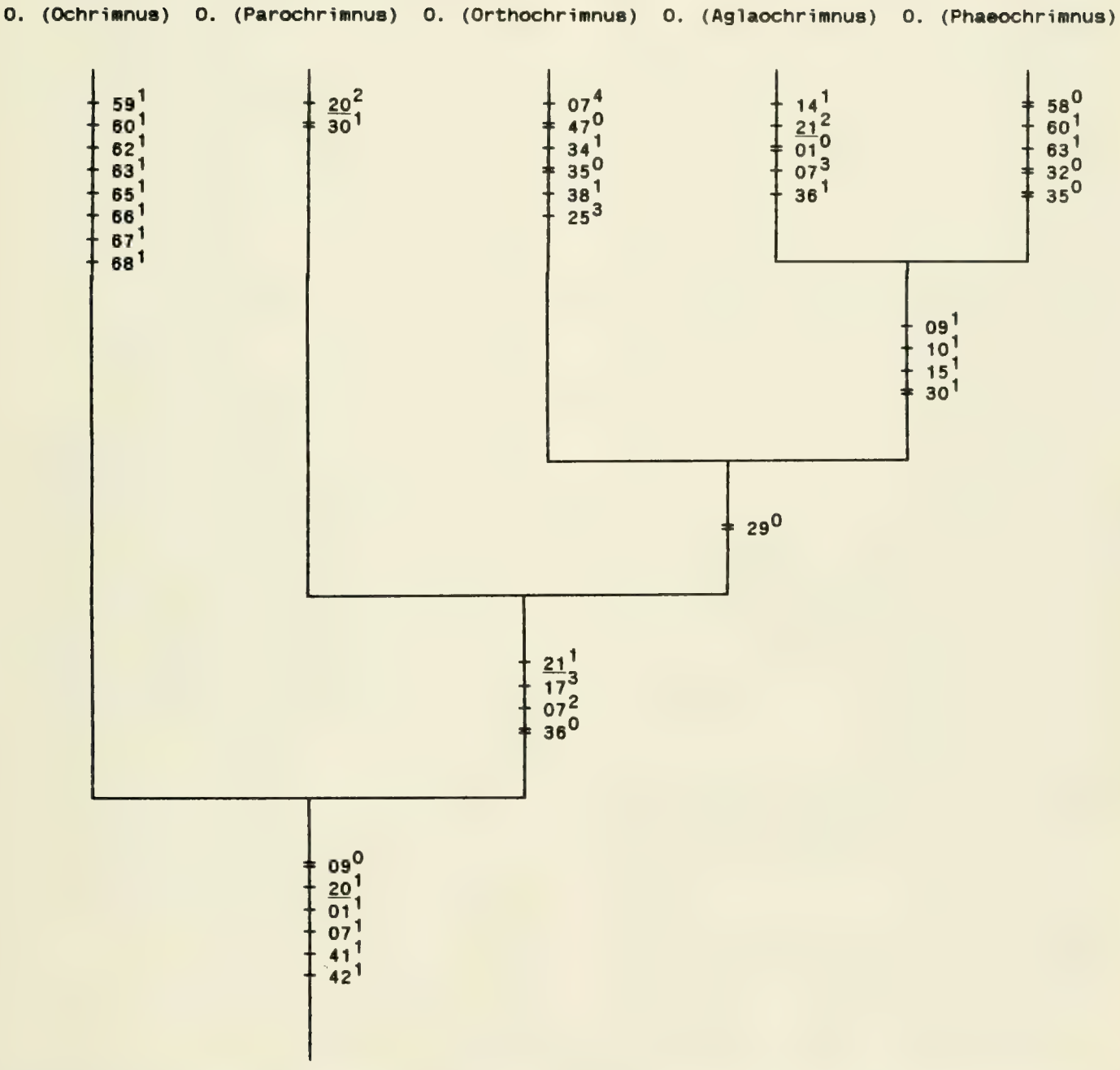


Fig. 34. Character distributions for subgenera of *Ochrimnus* Stål Underlined characters have a consistency index of 1.00. Changes to a more derived state are indicated by a single crossbar, those to a less derived state by a double crossbar. Superscripts indicate the character state.

be paraphyletic or even polyphyletic as presently constituted.

If the spine-bearing vesical lobes characteristic of *Ochrimnus* are homologous with the conjunctival lobes of *Ochrostomus* and its allies, the conjunctival lobes of *Ochrimnus* (*Aglaochrimnus*) and *Ochrimnus* (*Phaeochrimnus*) should actually be considered a separate character. This interpretation would reduce the homoplasy apparent in characters 9 and 10.

LITERATURE CITED

Ashlock, P. D. 1957. An investigation of the taxonomic value of the phallus in the Lygaeidae (Hemiptera-Heteroptera). Ann. Entomol. Soc. America 50:407-426.

———. 1967. A generic classification of the Orsillinae of the world (Hemiptera-Heteroptera: Lygaeidae). Univ. California Publ. Entomol. 48. 82p.

———. 1975. Toward a classification of North American Lygaeinae

(Hemiptera-Heteroptera: Lygaeidae). J. Kansas Entomol. Soc. 48:27-32.

Barber, H.G. 1914. New Hemiptera-Heteroptera with comments upon the distribution of certain known species. J. New York Entomol. Soc. 22:164-171.

———. 1921. Revision of the genus *Lygaeus* Fab. (Hemiptera-Heteroptera). Proc. Entomol. Soc. Washington 23:63-68.

———. 1923. A preliminary report on the Hemiptera-Heteroptera of Porto Rico collected by the American Museum of Natural History. American Mus. Nov. 75. 13p.

———. 1947. The family Lygaeidae (Hemiptera-Heteroptera) of the island of Cuba and the Isle of Pines. Mem. Soc. Cubana Hist. Natur. 19:55-75.

———. 1948. Lygaeidae collected in western Texas, with a new Lygaeospilus from California. Ohio J. Sci. 48:66-68.

Barber, H. G., and P. D. Ashlock. 1960. The Lygaeidae of the Van Voast - American Museum of Natural History expedition to the Bahama Islands 1953. Proc. Entomol. Soc. Washington 62:117-124.

Berg, C. 1879. Hemiptera Argentina enumeravit speciesque novas descripsit. Buenos Aires: Pauli E. Coni. 316p.

———. 1883. Addenda et emedanda ad Hemiptera Argentina. An. Soc. Cient. Argentina 15:241-269.

Bergroth, E. 1893. Notes hémiptèrologiques. Rev. Entomol. Caen 12:153-155.

Blanchard, É. 1840. Histoire naturelle des insectes Orthoptères, Neuroptères, Hémiptères, Hymenoptères, Lépidoptères et Diptères. Vol. III. Paris: P. Dumeril.

———. 1852. Hemipteros. pp. 113-320. *In* C. Gay, Historia fisica y politica de Chile. Zoologica. Vol. 7. Paris: author. 471p.

Brailovsky, H. 1975. Contribución al estudio de los Hemiptera-Heteroptera de México: VII. Distribución y diagnosis de las especies del género *Melanopleurus* Stål (Lygaeidae-Lygaeinae) y descripción de dos nuevas especies. An. Inst. Biol. Univ. Nal. Autón. México 46, Ser. Zool. (1):53-62.

———. 1977a. Una nueva especie del género *Neacoryphus* (Hemiptera-Heteroptera-Lygaeidae-Lygaeinae) de Costa Rica. An. Inst. Biol. Univ. Nal. Autón. México 48, Ser. Zool. (1):93-96.

———. 1977b. Contribución al estudio de los Hemiptera-Heteroptera de Mexico. XII. El género *Neacoryphus* Scudder (Lygaeidae-Lygaeinae) y descripción de tres nuevas especies. An. Inst. Biol. Univ. Nal. Autón. México 48, Ser. Zool. (1):97-122.

———. 1977c. Contribución al estudio de los Hemiptera Heteroptera de México. XIII. Revisión del género *Acroleucus* Stål (Lygaeidae-Lygaeinae) con descripción de una nueva especie. An. Inst. Biol. Univ. Nal. Autón. México 48, Ser. Zool. (1):123-128.

———. 1977d. Una nueva especie del género *Melanopleurus* Stål (Hemiptera-Heteroptera-Lygaeidae-Lygaeinae) de California, Estados Unidos de Norteamerica. An. Inst. Biol. Univ. Nal. Autón. México 48, Ser. Zool. (1):129-132.

———. 1978a. Un nuevo género y una nueva especie de Lygaeinae (Hemiptera-Heteroptera-Lygaeidae) del Perú. An. Inst. Biol. Univ. Nal. Autón. México 49, Ser. Zool. (1):115-122.

———. 1978b. Estudio del género *Lygaeus* Fabricius 1794, del nuevo mundo, con descripción de cinco nuevas especies (Hemiptera-Heteroptera-Lygaeidae-Lygaeinae). An. Inst. Biol. Univ. Nal. Autón. México 49, Ser. Zool. (1):123-166.

———. 1979a. Seis nuevas especies del género *Melanopleurus* Stål (Hemiptera-Heteroptera-Lygaeidae-Lygaeinae). An. Inst. Biol. Univ. Nal. Autón. México 50, Ser. Zool. (1):193-204.

———. 1979b. Revisión del género *Craspeduchus* Stål, con descripción de dos nuevas especies (Hemiptera-Heteroptera-Lygaeidae-Lygaeinae). An. Inst. Biol. Univ. Nal. Autón. México 50, Ser. Zool. (1):205-226.

———. 1979c. El género *Neacoryphus* Scudder en Sudamérica y descripción de tres nuevas especies (Hemiptera-Heteroptera-Lygaeidae-Lygaeinae). An. Inst. Biol. Univ. Nal. Autón. México 50, Ser. Zool. (1):227-239.

———. 1980. Revisión del género *Acroleucus* Stål (Hemiptera-Heteroptera-Lygaeidae-Lygaeinae). Folia Entomol. Mexicana 44:39-120.

———. 1982a. Revision del complejo *Ochrimnus*, con descripción de nuevas especies y nuevos géneros (Hemiptera-Heteroptera-Lygaeidae-Lygaeinae). Folia Entomol. Mexicana 51:(1)-(163).

———. 1982b. Un nuevo arreglo nomenclatorial y descripción de tres nuevos géneros y dos nuevas especies Americanas de la subfamilia Lygaeinae (Hemiptera-Heteroptera-Lygaeidae). An. Inst. Biol. Univ. Nal. Autón. México 52 (1981), Ser. Zool. (1):259-276.

———. 1982c. Revisión del género *Biblochrimnus* Brailovsky (Hemiptera-Heteroptera-Lygaeidae-Lygaeinae). An. Inst. Biol. Univ. Nal. Autón. México 52 (1981), Ser. Zool. (1):289-299.

———. 1983a. Note. Folia Entomol. Mexicana 56:103.

———. 1983b. Revisión del género *Torvochrimnus* Brailovsky (Hemiptera-Heteroptera-Lygaeidae-Lygaeinae) con descripción de dos nuevas especies. An. Inst. Biol. Univ. Nal. Autón. México 53 (1982), Ser. Zool. (1):285-320.

———. 1984a. Nuevas adiciones al género *Acroleucus*, Stål (Hemiptera-Heteroptera-Lygaeidae-Lygaeinae). An. Inst. Biol. Univ. Nal. Autón. México 54 (1983), Ser. Zool. (1):35-52.

———. 1984b. Revisión del género *Dalmochrimnus* Brailovsky (Hemiptera-Heteroptera-Lygaeidae-Lygaeinae). An. Inst. Biol. Univ. Nal. Autón. México 55, Ser. Zool. (1):183-194.

———. 1984c. Revisión del género *Latochrimnus* Brailovsky (Hemiptera-Heteroptera-Lygaeidae-Lygaeinae). An. Inst. Biol. Univ. Nal. Autón. México 55, Ser. Zool. (2):111-128.

———. 1984d. Revisión del género *Malleochrimnus* Brailovsky (Hemiptera-Heteroptera-Lygaeidae-Lygaeinae). An. Inst. Biol. Univ. Nal. Autón. México 55, Ser. Zool. (2):129-142.

Brailovsky, H., and E. Barrera. 1984. Cinco especies nuevas, nuevos datos distribucionales y notas biológicas acerca de Lygaeinae Americanos (Lygaeidae: Hemiptera: Heteroptera). An. Inst. Biol. Univ. Nal. Autón. México 55, Ser. Zool. (2):95-110.

Brailovsky, H., and J. S. Brailovsky. 1979. Una nueva especie del género *Nicuesa* Distant (Hemiptera-Heteroptera-Lygaeidae-Lygaeinae) de Perú. An. Inst. Biol. Univ. Nal. Autón. México 50, Ser. Zool. (1):251-254.

Breddin, G. 1904. Neue Rhynchotenausbeute aus Süd-Amerika. Soc. Entomol. 18:147-149.

———. 1912. Hemiptera tria neotropica. Entomol. Mitt. 1:351-354.

Cobben, R. H. 1968. Evolutionary trends in Heteroptera. Part I. Eggs, architecture of the shell, gross embryology and eclosion. Wageningen: Agricultural Research Reports. 707. 475p.

Costa, A. 1862. Aumenti del Museo da Novembre 1860 a Dicembre 1861. Ann. Mus. Zool. Univ. Napoli 1:11-40.

Curtis, J. 1833. British Entomology, ... 10: plts. 434-481. London: author.

Dallas, W. S. 1852. List of the Specimens of Hemipterous Insects in the Collection of the British Museum. Part II. London: Taylor & Francis Inc. 224p.

Davis, N. T. 1961. Morphology and phylogeny of the Reduvioidea (Hemiptera: Heteroptera). Part II. Wing Venation. Ann. Entomol. Soc. America 54:340-354.

DeGeer, C. 1773. Mémoires pour servir à l'histoire des insectes. Vol. 3. Stockholm: Pierre Hasselberg. 696p.

Distant, W. L. 1882. Lygaeidae. pp. 173-220. *In* F. D. Godman and O. Salvin (eds), Biologia Centrali-Americana. Zoologia. Insecta. Rhynchota. Hemiptera-Heteroptera. Vol. I. London: Dulau & Co. 462p.

———. 1892 A Naturalist in the Transvaal. London: R. H. Porter. 277p.

———. 1893 Lygaeidae. pp. 378-462. *In* F. D. Godman and O. Salvin (eds), Biologia Centrali-Americana. Zoologia. Insecta. Rhynchota. Hemiptera-Heteroptera. Vol. I. Supplement. London: Dulau & Co. 462p.

———. 1901. Rhynchotal notes. X. Heteroptera: Family Lygaeidae. Ann. Mag. Natur. Hist. ser. 7, 7:531-541.

———. 1904. Fauna of British India, including Ceylon and Burma. Rhynchota. Vol. 2. (Heteroptera). London: Taylor & Francis. 503p.
Erichson, W. F. 1842. Beitrag zur Insekten-fauna von Vandiemens-land mit besonderer Berücksichtigung der geographischen Verbreitung der Insekten. Arch. Naturgesch. 8:83-287.
———. 1848. Hemiptera-Heteroptera. pp. 609-614. *In* M. R. Schomburgk, Reisen in Britisch Guiana in den Jahren 1840-1844 im auftrag Sr. Majestät des Königs von Pruessen ausgeführt von Richard Schomburgk. Vol. 3. Leipzig: Weber.
Fabricius, J. C. 1775. Systema entomologiae ... Flensburgi et Lipsiae: Korte. 832p.
———. 1781. Species insectorum ... Vol. 2. Hamburg et Kilonii: Ernst Bohni. 832p.
———. 1794. Entomologia systematica ... Vol. 4. Hafniae: C. G. Proft. 472p.
———. 1803. Systema Rhyngotorum ... Brunsvigae: Apud Carolum Reichard. 314p.
Fallou, G. 1891. Diagnoses d'Hémiptères nouveaux. Rev. Entomol. Caen 10:5-10.
Froeschner, R. C. 1979. Heteroptera in an oft-overlooked paper of P. R. Uhler (Hemiptera). Proc. Entomol. Soc. Washington 8:653-656.
Gorski, L. J. 1968. A new species of *Lygaeus* from Peru. (Hemiptera: Lygaeidae). Proc. Entomol. Soc. Washington 70:74-77.
Gmelin, J. F. 1790. Caroli a Linne. Systema naturae ... ed. 13, aucta, reformata. Vol. I. Part IV. Lipsiae: G. E. Beer. 707p.
Guérin-Méneville, F. É. 1844. Iconographie du regne animal de G. Cuvier. Vol. 3. Paris & London: J. B. Bailliere. 576p.
———. 1857. Animaux articules a pieds articules. pp. 328-358. *In* R. de la Sagra, Histoire physique, politique et naturelle de l'Isle de Cuba. Vol. 8. Paris: Arthus Bertrand. 868p.
Hahn, C. W. 1834. Die Wanzenartigen Insecten 2:33-120. Nürnberg: C. H. Zeh'schen Buchhandlung.
Hamilton, K. G. A. 1972a. The insect wing, part II. Vein homology and the archetypal insect wing. J. Kansas Entomol. Soc. 45:54-58.
———. 1972b. The insect wing, part III. Venation of the orders. J. Kansas Entomol. Soc. 45: 145-162.
———. 1972c. The insect wing, part IV. Venational trends and the phylogeny of the winged orders. J. Kansas Entomol. Soc. 45: 295-308.
Herrich-Schäffer, G. A. W. 1843. Die Wanzenartigen Insecten 7:17-40. Nürnberg: C. H. Zeh'schen Buchhandlung.
———. 1847. Die Wanzenartigen Insecten 8:101-130. Nürnberg: C. H. Zeh'schen Buchhandlung.
———. 1850. Die Wanzenartigen Insecten 9:188-217. Nürnberg: C. H. Zeh'schen Buchhandlung.
Kirkaldy, G. W. Hemiptera: new and old. No. 1. Canadian Entomol. 41:30-32.
Leston, D. 1953a. Notes on the Ethiopian Pentatomoidea (Hemiptera): XVI. An acanthosomid from Angola, with remarks upon the status and morphology of Acanthosomidae Stål. Publ. Cult. Comp. Diam. Angola 16:121-132.
———. 1953b. "Phloeidae" Dallas: Systematics and morphology with remarks on the phylogeny of "Pentatomoidea" Leach and upon the position of "Serbana" Distant (Hemiptera). Rev. Brasil Biol. 13:121-140.
———. 1962. Tracheal capture in ontogenetic and phylogenetic phases of insect wing development. Proc. R. Entomol. Soc. London (A) 37:135-144.
Linneaus, C. 1758. Systema naturae ... Ed. decima reformata. Vol. 1. Holmiae: Laurentii Salvii. 824p.
Maldonado-Caprilles, J. 1974. The neotropical genus *Melanopleurus* (Hemiptera: Lygaeidae). Proc. Entomol. Soc. Washington 76:22-30.
Montandon, A. L. 1893. Lygaeides exotiques. Notes et descriptions d'espèces nouvelles. Ann. Soc. Entomol. Belgique 37:399-406.
Mulsant, É., and C. Rey. 1878. Histoire naturelle des Punaises de France. Part V. Lygeides. Ann. Soc. Linn. Lyon (ns) 25:131-189. (also separately printed and paged)
Osborn, H. 1904. Notes on South American Hemiptera-Heteroptera. Ohio Natur. 5:195-204.
Parshley, H. M. 1919. On some Hemiptera from western Canada. Occ. Pap. Mus. Zool. Univ. Michigan 71. 35p.
Pimental, R. A., and R. Riggins. 1987. The nature of cladistic data. Cladistics 3:201-209.
Reuter, O. M. 1888. Revision synonymica Heteropterorum Palaearcticorum. Acta Soc. Sci. Fennica 15:548-88.
Say, T. 1825. Descriptions of new Hemipterous insects collected in the expedition to the Rocky Mountains, performed by order of Mr. Calhoun, Secretary of War, under command of Major Long. J. Acad. Natur. Sci. Philadelphia 4: 307-345.
———. 1831. Descriptions of new species of Heteropterous Hemiptera of North America. New Harmony, Indiana: author. 39p.
Schaefer, C. W. 1964. The morphology and higher classification of the Coreoidea (Hemiptera-Heteroptera): Parts I and II. Ann. Entomol. Soc. America 57:670-684.
———. 1972. Degree of metathoracic scent-gland development in the trichophorous Heteroptera (Hemiptera). Ann. Entomol. Soc. America 65:810-821.
———. 1975. Heteropteran trichobothria (Hemiptera: Heteroptera). Int. J. Insect Morphol. Embryol. 4:193-264.
Scudder, G. G. E. 1958. Results of the Oxford University Cayman Islands biological expedition of 1938: Lygaeidae (Hemiptera-Heteroptera). Entomol. Mon. Mag. 94:145-150.
———. 1963. A revision of the genus *Astacops* sensu lat. (Hemiptera: Lygaeidae). Pac. Ins. 5:315-415.
———. 1965. *Neacoryphus* Scudder, a new genus of Lygaeinae (Hemiptera: Lygaeidae). Proc. Entomol. Soc. British Columbia 62:34-37.
———. 1981. Two new species of Lygaeinae (Hemiptera: Lygaeidae) from Canada. Canadian Entomol. 113:747-753.
Seidenstücker, G. 1964. *Psileula mimica* n. gen. n. sp. und die mikropteren Lygaeinen (Heteroptera, Lygaeidae). Reichenbachia 2:199-207.
Signoret, V. 1860. Faune des Hémiptères de Madagascar. 2e Partie, Hétéroptères. Ann. Soc. Entomol. France (3) 8:917-972.
Slater, A. 1985. A taxonomic revision of the Lygaeinae of Australia (Heteroptera: Lygaeidae). Univ. Kansas Sci. Bull. 52:301-481.
———. 1988. A new genus and two new species of Lygaeinae (Heteroptera: Lygaeidae). J. Kansas Entomol. Soc. 61:308-316.
Slater, J. A. 1964a. A Catalogue of the Lygaeidae of the World. Vol. 1. Storrs, Connecticut: University of Connecticut, 778p.
———. 1964b. Hemiptera (Heteroptera): Lygaeidae. South African Anim. Life 10:15-228.
———. 1979. The systematics, phylogeny, and zoogeography of the Blissinae of the world (Hemiptera, Lygaeidae). Bull. American Mus. Nat. Hist. 165. 180p.
Slater, J. A., and H. W. Hurlbutt. 1957. A comparative study of the metathoracic wing in the family Lygaeidae. Proc. Entomol. Soc. Washington 59:67-79.
Snodgrass, R. E. 1935. Principles of Insect Morphology. New York: McGraw-Hill Book Company. 667p.
Stål, C. 1858. Bidrag till Rio Janeiro-Traktens Hemiptera-fauna. Kongl. Svenska VetenskAkad. Handl. 2:7:1-84.
———. 1862. Hemiptera Mexicana enumeravit speciesque novas descripsit. Stettiner Entomol. Zeitung 23:81-118,273-281,289-325,437-462.
———. 1867. Analecta Hemipterologica. Berliner Entomol. Zeitschrift 10:151-172,381-394.
———. 1868. Hemiptera Fabriciana. Kongl. Svenska VetenskAkad. Handl. 7(11):1-148.
———. 1872. Genera Lygaeidarum Europae disposuit. Öfvers. Kongl. VetenskAkad. Förh., Stockh. 29:37-62.
———. 1874. Enumeratio Hemipterorum. Part 4. Kongl. Svenska VetenskAkad. Handl. 12(1):1-186.
Štys, P. 1967. Monograph of Malcinae Acta Entomol. Mus. Nat. Pragae 37:
———. 1972. Two new genera and species of pteryopolymorphic

Lygaeinae from Ethiopea and W. Pakistan (Heteroptera, Lygaeidae). Acta Entomol. Bohemoslovacia 69:251-265.
Sweet, M. H. 1981. The external morphology of the pre-genital abdomen and its evolutionary significance in the order Hemiptera (Insecta). Rostria 33(Suppl.):41-51.
Swofford, D. L. 1985. PAUP. Phylogenetic Analysis Using Parsimony. Version 2.4. Champaign, Illinois: Illinois Natural History Survey. 75p.
Tanaka, T. 1926. Homologies of the wing veins of the Hemiptera. Annot. Zool. Japan 11:33-57.
Torre-Bueno, J. R. 1944. New records of *Oncopeltus* (Hemiptera, Lygaeidae) and a new species from the U. S. Bull. Brooklyn Entomol. Soc. 39:135-136.
Ueshima, N. 1979. Hemiptera II: Heteroptera. *In* J. Bernard (ed.), Animal Cytogenetics 3: Insecta 6. Berlin: Gebrüder Borntraeger. 117p.
Ueshima, N., and P. D. Ashlock. 1980. Cytotaxonomy of the Lygaeidae (Hemiptera-Heteroptera). Univ. Kansas Sci. Bull. 51:717-801.
Uhler, P. R. 1869. Notices of the Hemiptera obtained by the expedition of Prof. James Orton in Ecuador and Brazil. Proc. Boston Soc. Natur. Hist. 12:321-327.
———. 1872. Notices of the Hemiptera of the western territories of the United States chiefly from the surveys of Dr. F. V. Hayden. pp. 392-423. *In* F. V. Hayden, Prelim. Rept. U. S. Geol. Surv. Montana.
———. 1893. Hemiptera Heteroptera of the Death Valley Expedition. North American Fauna 7:260-265.
———. 1894. Observations upon the Heteropterous Hemiptera of Lower California, with descriptions of new species. Proc. California Acad. Sci. (2):4:223-295.
Van Duzee, E. P. 1907. Notes on Jamaican Hemiptera. Bull. Buffalo Soc. Nat. Sci. 8:1-79.
———. 1909. North American Heteroptera. Entomol. News 20:231-234.
———. 1914. A preliminary list of the Hemiptera of San Diego County, California. Trans. San Diego Soc. Natur. Hist. 2:1-57.
———. 1916. Check List of the Hemiptera (Excluding the Aphididae, Aleurodidae and Coccidae) of America, North of Mexico. New York: New York Entomological Society. 111p.
———. 1929. Some new western Hemiptera. Pan-Pac. Entomol. 5:186-191.
Walker, F. 1872. Catalogue of the Specimens of Hemiptera Heteroptera in the Collection of the British Museum. Part 5. London: British Museum (Natural History). 202p.
Wooten, R. J., and C. R. Betts. 1986. Homology and function in the wings of Heteroptera. Syst. Entomol. 11:389-400.

ADDENDUM

The following publication should also be cited:

Alayo, P. D. 1973. Los Hemipteros de Cuba. Parte XI. Familia Lygaeidae. Torreia (N.S.) 25. 79p.

The names *Lygaeus dearmasi* Alayo, 1973, and *Lygaeus wygodzinskyi* Alayo, 1973, should be added to the list of *incertae sedis* species of *Lygaeus*.

ANNOUNCEMENT

The *University of Kansas Science Bulletin* (continuation of the *Kansas University Quarterly*) is an outlet for scholarly scientific investigations carried out at the University of Kansas or by University faculty and students. Since its inception, volumes of the *Bulletin* have been variously issued as single bound volumes, as two or three multi-paper parts or as series of individual papers. Issuance is at irregular intervals, with each volume prior to volume 50 approximately 1000 pages in length. Effective with volume 50, page size has been enlarged, reducing the length of each volume to about 750 pages.

The supply of all volumes of the *Kansas University Quarterly* is now exhausted. However, most volumes of the *University of Kansas Science Bulletin* are still available and are offered, in exchange for similar publications, to learned societies, colleges and universities and other institutions, or may be purchased at $30.00 per volume. Where some of these volumes were issued in parts containing several papers, the individual parts are priced at the rate of 3 cents per page plus postage. Current policy, initiated with volume 46, is to issue individual papers as published. Such separata may be purchased individually at the rate of 7 cents per page, with a minimum charge of $1.50 per separate, plus postage. Subscriptions for forthcoming volumes may be entered at the rate of $30.00 per volume. All communications regarding exchanges, sales and subscriptions should be addressed to the EXCHANGE LIBRARIAN, UNIVERSITY OF KANSAS LIBRARIES, LAWRENCE, KANSAS 66045.

Reprints of individual papers for personal use by investigators are available for most recent and many older issues of the *Bulletin*. Such requests should be directed to the author.

The International Standard Serial Number of this publication is US ISSN 0022-8850.

Editor
Charles D. Michener

Editorial Board
Meredith Lane, *Chairman*
James S. Ashe
George W. Byers
Christopher Haufler
Norman A. Slade

THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. 55, No. 2, pp. 57–96 January 29, 1993

JAN 28 1993
HARVARD UNIVERSITY

Autumnal Mecoptera of Southeastern United States[1]

George W. Byers

CONTENTS

Abstract 57
Introduction 58
Acknowledgments 58
Three new terms 59
Species groups 59
Family Meropeidae (*Merope tuber*) 60
Family Bittacidae (*Bittacus occidentis, B. texanus*) 60
Family Panorpidae
Panorpa lugubris group (*lugubris*, 61; *nuptialis*, 62; *rufa*, 62; *floridana*, 63) 61
Panorpa virginica group (*virginica*, 65; *neglecta*, 65; *oconee*, 66; *choctaw*, 66 65
Ungrouped species (*bichai*, 70; *bifida*, 70; *braueri*, 72; *isolata*, 72; *americana*, 72) 70
Panorpa banksiana group (*gracilis*, 72; *palustris*, 73; *banksiana*, 73) 72
Panorpa rufescens group (*hispida*, 73; *scopulifera*, 76; *rufescens*, 77; *ferruginea*, 78; *confinis*, 80; *pachymera*, 82; *acuminata*, 84; *rupeculana*, 86; *venosa*, 88; *vernalis*, 88; *planicola*, 91; *robusta*, 91) 73
Unusual autumnal records (*anomala*, 92; *insolens*, 92; *longicornis*, 92; *nebulosa*, 92; *speciosa*, 92) 92
Key to autumnal Mecoptera of the southeastern United States 93
Literature cited 96

ABSTRACT

Thirty-three species of Panorpidae, two of Bittacidae and one of Meropeidae known to have an autumnal period of adult emergence in the southeastern United States are reviewed. Included are the following new species of *Panorpa*: *acuminata*, *bichai*, *choctaw*, *confinis*, *ferruginea*, *floridana*, *hispida*, *oconee*, *pachymera*, *planicola*, *rupeculana* and *scopulifera*. Rediscovery of *Panorpa neglecta* and *P. gracilis* is recorded, as well as range extensions for several other species. Observations on ecological occurrence are given for most species. A neotype is designated for *Panorpa rufescens* Rambur. *Panorpa venosa* Westwood is removed from synonymy of *P. rufescens*. All known autumnal species of the region are differentiated in a taxonomic key.

[1]Contribution no. 3085 from the Snow Entomological Museum and Department of Entomology, University of Kansas, Lawrence, Kansas 66045-2119

INTRODUCTION

Many species of North American Mecoptera apparently are univoltine, with adults on the wing in late spring and summer. Numerous others for which an extended flight period has been somewhat vaguely described (e.g., "June - October") turn out to be bivoltine. Adults of *Panorpa anomala* and *P. helena*, for instance, appear in floodplain woods and later in more upland woods in eastern Kansas from about mid-May to early July and reappear in late August and early September. In most of July and August they are competely absent in habitats where they are common earlier and later. Laboratory rearing suggests that the smaller late-summer generation consists of the more rapidly maturing offspring of the spring generation and that more slowly developing individuals from eggs laid in spring (particularly late in spring) reach adulthood the next spring.

Flight periods of *Panorpa* appear to be correlated with fairly cool weather; bivoltine species in the southern United States have, in general, an earlier spring generation than those at the latitude of Kansas but a later second generation that is autumnal.

In contrast, adults of a few species have been collected more frequently in the autumn, while occasional specimens taken in spring are recorded. Such species include *Panorpa lugubris*, *P. nuptialis* and *P. rufa*, which comprise a structurally, phylogenetically distinct species group.

"Autumnal," as used here, refers to the calendar definition of autumn, 21 September to 22 December. However, depending on the location within the vast area under consideration, the autumnal equinox can be quite hot and summer-like or, conversely, cool and occasionally with chilly nights. And the winter solstice can vary from balmy in northern Florida to altogether wintery in, say, Missouri and Kentucky.

To study these autumnal species in their natural habitats and to determine whether there is an autumnal period of emergence in certain little-known species, I travelled to the southeastern United States in the fall of 1977 (21 September - 10 October). The following account reports the results of that trip and of occasional others, as well as data gathered from the study of various institutional and private collections.

The area covered by this report is from the Atlantic coast westward to approximately the 98th meridian (98°W) and southward from about the 39th parallel (39°N)—a line roughly indicated by Washington, D.C., Cincinnati, St. Louis and Kansas City. This southeastern quarter of the contiguous United States includes most of the Atlantic Coastal Plain, the Gulf Coastal Plain, the piedmont of the Appalachian Mountains (there being no autumnal records from the mountains), the lower Mississippi Valley and the Ozark Plateau.

Methods: Drawings were made with the aid of a camera lucida. Those that are shaded were made on coquille-board. When terminal segments were removed and dissected, the parts were subsequently mounted in polyvinyl alcohol (with lacto-phenol) on a point of 2-ply Bristol-board marked "in P.V.A." and placed on the pin beneath the specimen. This plastic mounting medium preserves the parts and protects them from dust but is soluble in warm water so that the parts can, in the future, be readily removed and studied "in the round."

Experience has shown that the usual textbook directions for pinning specimens are not suited to either scorpion-flies (Panorpidae) or hanging-flies (Bittacidae). Due to the backward deflection of the thoracic segments of scorpion-flies, a pin inserted vertically through the mesonotum usually emerges in front of the middle coxae, where the thorax is quite thin and weak. This often results in breakage of dried specimens at the level of the pin. I recommend pinning through the metanotum so the pin will emerge between the middle and hind coxae; this places the pin through the thickest, strongest part of the thorax. Bittacids pinned through the small thorax are ordinarily left with dangling long legs that are easily broken subsequently during the labelling process. Drying bittacids more or less flat in paper envelopes, with the legs arranged compactly, and then mounting them on the left side on a Bristol-board point overcomes this problem. Admittedly, specimens so prepared require more space in the collection, but they are also much more likely to remain intact over time.

Mr. Wesley (Wes) Bicha, of Oliver Springs, Tennessee, has been a very important contributor to our knowledge of the distribution of North American Mecoptera. In the lists of collection data hereinafter, most specimens taken by him are designated simply by "WB" as collector. My own collections are similarly indicated as made by "GWB."

Types: Most of the holotypes and allotypes and some of the paratypes of the new species described here are deposited in the Snow Entomological Museum (SEM) at the University of Kansas, Lawrence, Kansas. Most of the paratypes collected by Wes Bicha are returned to him (WB); paratypes of most new species are also deposited in the U.S. National Museum of Natural History, Washington, D.C. (USNM), the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ) and the Museum of Zoology, University of Michigan, Ann Arbor, Michigan (UMMZ).

ACKNOWLEDGMENTS

The 1977 trip on which most of the specimens dealt with here were collected was supported in part by grant DEB-77-15868 from the National Science Foundation. I am grateful for this assistance. The very important contribution of specimens by Mr. Wes Bicha, by loan and by gift to the Snow Entomological Museum, has already been mentioned but cannot be overemphasized. For the loan of specimens in their care, I thank Dr. Oliver S. Flint, Jr., of the National Museum of Natural History, Washington, D.C.; Dr. Howard V. Weems, Jr., Florida State Collection of Arthropods, Gainesville; Ms. Cleone T. Graham, Museum of Comparative Zoology, Harvard University, Cambridge; Dr. Stephen J. Brooks, The Natural History Museum, London; Dr. T. L. Schiefer, Mississippi Entomological Museum; Dr. Laurent LeSage, Agriculture Canada, Ottawa; and Mr. Bryant Mather, Clinton, Mississippi. For assistance with place names in their respective states, I am indebted to reference librarians Carol M. Tobin, University of South Carolina, and Jay Evatt, University of Georgia. Professor Oliver Phillips, Department of Classics, University of Kansas, kindly checked my proposed names for new species. For a variety of useful comments, I am indebted to Dr. Charles D. Michener, Snow Entomological Museum. The paper was originally entered into computer by Ms. Jan Elder, revisions entered by Ms. Judy Wiglesworth.

LIBRARY
JAN 28 1993

HARVARD UNIVERSITY

THREE NEW TERMS

1. *Humeral spots.* In the following taxonomic descriptions of *Panorpa* species, reference is made to the dark brown bands and spots on the wings. Their pattern is usually consistent within a species, although examples of striking variation are known (e.g., in *P. debilis*). Since the fore wings often broadly overlap the hind wings and thus obscure them, in life as well as in specimens that have not had the wings spread, the pattern of the fore wings only is ordinarily described. The markings on the hind wings are generally less extensive than those of the fore wings.

Esben-Petersen (1921: 12, fig. 1) diagrammed a wing of *Panorpa* and gave names to various bands and spots, based in part on names used by earlier authors. Carpenter (1931: 220, fig. 3) followed Esben-Petersen in most of these names. He introduced the term "marginal spots" for two small spots between the costa and the subcosta or radius, in the humeral part of the wing. Esben-Petersen, however, had used "marginal spot" for an often much larger spot between the pterostigmal and basal bands (Fig. 1). Carpenter omitted this spot from his diagram, just as Esben-Petersen had omitted the smaller spots from his illustration.

To put an end to this confusion, I propose that the "marginal spots" in Carpenter's terminology be called *humeral spots* and that "marginal spot" be used as in Esben-Petersen's system. This is the terminology adopted hereinafter.

2. *Aedeagal hamulus.* This term is introduced to replace such cumbersome wording as "a short, thick, upturned process at base of aedeagus, below ventral valves" (Byers, 1973a: 368-369), or projections from the ventral parameres "fused basally to form two narrow elongate extensions" (Webb, 1974: 172). The structure, at the mid-ventral base of the aedeagus (Fig. 2, ah), usually has a less distinct connection to the ventral parameres than shown by Webb. It is almost always upturned, hence the term *aedeagal hamulus* (hook). In some species it has a single, blunt (rounded or truncate) tip; in others there are two pointed branches, diverging to varying degrees. Absent in still others but usually readily visible when present, the *aedeagal hamulus* has species-specific shapes and is thus a taxonomically useful structure. (Its function in those species that possess it has not been determined.)

3. *Basistylar flanges.* In males of most species of *Panorpa*, there is, on the ventro-mesal surface of each basistyle, a somewhat blade-like or fin-like projection against which the lateral process of the aedeagus abuts. These projections have been described as prominent humps, large lobes, prominent lobes, large humps, etc. (Carpenter, 1931); clearly, Carpenter noticed that the shapes of these structures varied among species while being fairly constant within a species. But a term that recognizes their essentially two-dimensional nature seems to me more accurately descriptive than "hump" or "lobe." Accordingly, I propose "basistylar flanges" (Fig. 2, bf). Their shape varies from low with virtually straight or truncate margin to wide and rounded, nearly semicircular.

SPECIES GROUPS

Most of the species of Panorpidae in the southeastern states can be assigned to four species groups based upon morphological similarities. Since these groups, with one exception, do not correspond to the species groups recognized by Carpenter (1931:221), they may be briefly characterized as follows:

Panorpa lugubris group. This is the *lugubris* group as defined by Carpenter (that is, *lugubris*, *nuptialis* and *rufa*), except that I have added one species (*floridana*). Abdominal segments 7 and 8 in the male are proportionately longer than in other regional Panorpas. The dististyles are slender in the apical half; the apex of the ninth tergum is narrowly rounded or acute; and the hypovalves of the ninth sternum are short and borne on a common pedicel. The axial portion of the genital plate in the female is thick and projects beyond the posterior margin of the distal plate. This group appears to have close relationships with several species in Mexico.

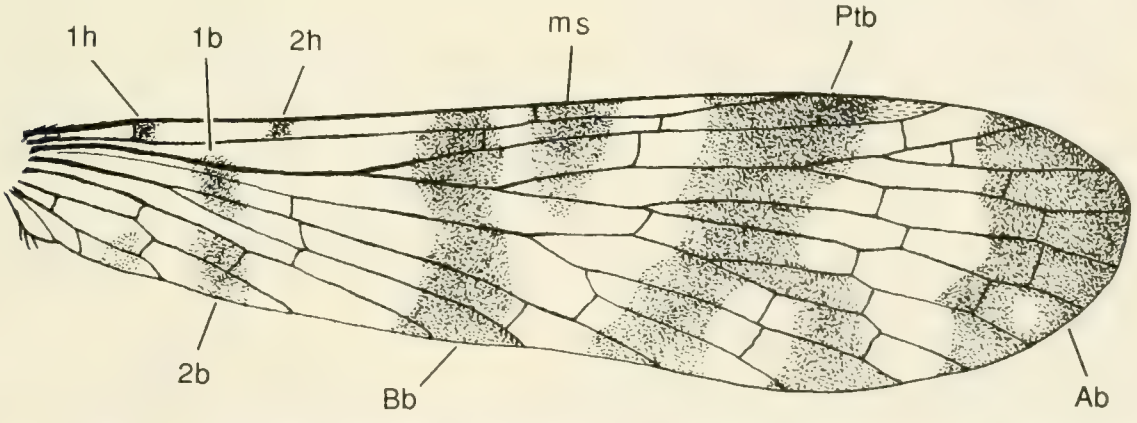


Fig. 1. Nomenclature of wing markings in *Panorpa*. Abbreviations: **Ab** - apical band, **Bb** - basal band, **Ptb** - pterostigmal band, **ms** - marginal spot, **1b** - first basal spot, **2b** second basal spot, **1h** - first humeral spot, **2h** - second humeral spot.

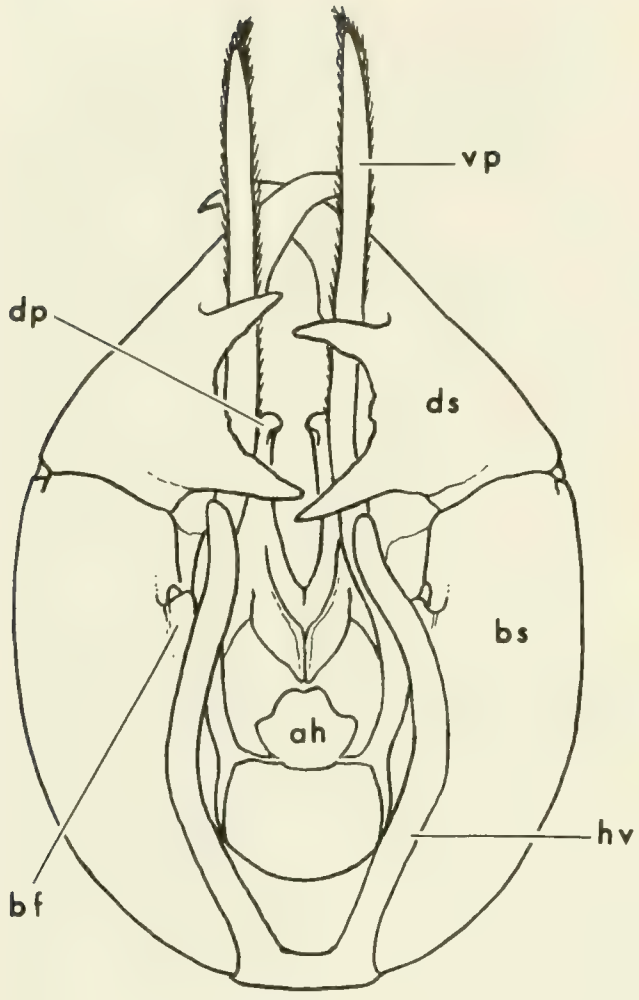


Fig. 2. Nomenclature of parts of genital bulb of male *Panorpa*. Abbreviations: **ah** - aedeagal hamulus, **bf** - basistylar flange, **bs** - basistyle, **dp** - dorsal paramere, **ds** - dististyle, **hv** - hypovalve (prolongation of ninth abdominal sternum), **vp** - ventral paramere.

Panorpa virginica group. Included in the *rufescens* group by Carpenter (1931), these species are characterized, in males, by long, slender hypovalves, ventral parameres extending between the dististyles, the aedeagal hamulus prominent but blunt and upturned apically, and the basal cups of the dististyles deep and opening generally mesad. In females, the basal plate of the genital plates is narrower than the distal plate, and there are well developed, darkly sclerotized laterotergites between the ninth abdominal tergum and the subgenital plate. In this group, besides *virginica*, are *neglecta*, *hungerfordi* and two new species, *choctaw* and *oconee*.

Panorpa banksiana group. These four species (*banksiana*, *dissimilis*, *gracilis* and *palustris*) are separated from Carpenter's *rufescens* group mainly on the basis of the males' shallow, ventrally-directed basal cups of the dististyles and the females' lack of anterior apodemes on the genital plate. *Panorpa carolinensis* and *P. longicornis* do not appear to belong to this group despite some conspicuous similarities in the females.

Panorpa rufescens group. Nearly all species in this group have essentially the same wing pattern as *rufescens* (i.e., apical band including some pale spots, pterostigmal band complete but not forked posteriorly, marginal spot usually interrupted between R_{2+3} and R_{4+5}, basal band interrupted near its mid-length, and first basal and first humeral spots present). A southeastern species lacking this pattern is *P. vernalis*, which has essentially unbanded wings. In males of the *rufescens* group, the basal cups of the dististyles are shallow with a narrow, darkly slcerotized border produced slightly as a dorso-mesal angle, or tooth, and with a row of short, thick, black setae along the dorsal margin near the base of the dististyle. There is no aedeagal hamulus. The ventral parameres are quite variable within the group but generally consistent within a species. Within the seasonal and geographical scope of this paper, the included species are *rufescens*, *ensigera*, *robusta*, *venosa* and *vernalis*, as well as several new species (*hispida*, *scopulifera*, *ferruginea*, *confinis*, *pachymera*, *acuminata*, *rupeculana* and *planicola*).

The *Panorpa nebulosa* group of Carpenter (1931) is made up of species outside the *lugubris* group in which males have no horn-like posterodorsal projection on the sixth abdominal segment. The wings usually have no complete bands or large spots, an uncommon condition in other species groups. But this is otherwise a diverse assemblage of species, as judged by details of male and female genitalic structures. With the exception of an October specimen of *nebulosa* from Missouri, there are no autumnal records of this group known to me from the southeastern states.

FAMILY MEROPEIDAE

Merope tuber Newman

Previously recorded from as far west as Columbia, Missouri, and eastern Minnesota (Byers, 1973b), *Merope tuber* has in recent years been collected in northeastern Kansas (Douglas Co.), eastern Oklahoma (Latimer Co.) northwestern Arkansas (Washington Co.), and eastern Iowa (Jones Co., outside the geographical scope of this paper). In Kansas, several individuals have been taken in Malaise traps set in the Breidenthal Reserve (University of Kansas), about two miles north of Baldwin City. The habitat is mixed deciduous woods near a stream that flows almost continuously, forming ponds in late summer in some years. The original collections were on 17 September 1981 (1m, 1f) and 7 October 1981 (1m, 1f), in a trap set for ichneumonids by David Wahl. Subsequent collections in various years have been within this span of dates and include specimens from Malaise traps I set considerably farther from the stream. The specimens trapped by Karl Stephan in Oklahoma were taken in August. Those collected by flight-intercept trap near Fayetteville, Arkansas, by Chris Carlton, are more nearly autumnal (5-12 September 1992).

FAMILY BITTACIDAE

Bittacus occidentis Walker

In some years, this is a common autumnal species in and near Lawrence, Kansas; but in other years it is seldom seen. Clearly at-

tracted to lights but apparently not particularly to other insects concentrated there, it usually does not capture prey but hangs motionless on walls, window frames and other illuminated surfaces, flying from time to time when disturbed by moths, beetles and other insects. On 22 September 1964, I collected 12 males and 14 females at lights on one building of the University of Kansas. Setty (1940) mentioned the attraction of *B. occidentis* to lights, and I have recorded some of his further observations as well as other occurrences of this species at lights (Byers, 1954).

Perhaps it is only coincidental, but the three most recent years of conspicuous abundance of *B. occidentis* in Kansas have been seven years apart (1978, 1985, 1992). This is in agreement with the 1964 "outbreak" noted above. In 1992, the peak of flight activity was in late August and early September (27 Aug. -8 Sept.), not truly autumnal.

Bittacus occidentis has an unusually extensive range: from New York southward to South Carolina and Alabama and southwestward to Nebraska, southern Texas (e.g., Sinton, San Patricio Co., 7 Oct.) and Arizona. There are numerous summer records, yet *occidentis* seems to be primarily autumnal. Carpenter (1931) listed autumnal collections of *occidentis* from Washington, D.C., North Carolina (Raleigh) and Alabama (Auburn). In recent years, I have seen autumnal specimens from Missouri (Boone Co., Columbia, 24-25 Sept., 9-20 Oct.), North Carolina (Wake Co., 4 Nov.), and Oklahoma (Payne Co., 21-29 Sept., 3-10 Oct.), in addition to the southern Texas collection already mentioned. The collection of this bittacid near universities where entomology is taught is probably a result of the need for people with an interest in Mecoptera to be in school rather than away on a field trip.

Bittacus texanus Banks

Although primarily an autumnal species, *B. texanus* like the similar but smaller *B. occidentis* has been collected in late spring and summer as well. Having reported the species from Lawrence, Kansas, nearly 500 miles north of its previously known range (Byers, 1954), I searched for it yearly but in vain from 1956 to 1980 in the vicinity of Lawrence. Following a relatively cool summer of abundant and evenly-spaced rains in 1981, I found *texanus* on a south-facing slope near the dam at Clinton Lake, a reservoir 4 miles west of Lawrence. The insects were found most often in the shade of shrubs and small trees and, late in the day, in nearby sweet clover (*Melilotus*) and grasses about two feet high. About 75 adults were collected on 6, 7, 10 and 13 September.

I have watched for the species every year since 1981 in this same area, as well as in other apparently suitable places near Lawrence, in summer and autumn, but have not seen it again. *B. texanus* has not been found common anywhere but is known also from scattered localities in eastern Texas (Cameron, Cherokee, Nacogdoches, Travis and Wise counties in late September and October), and western New Mexico (a single individual, from El Morro National Monument). Carpenter (1931:264) recorded a single female of the species from Citrus Center, Florida (Glades Co., west side of Lake Okeechobee), but I think the locality-date label must have been in error.

FAMILY PANORPIDAE

Panorpa lugubris Swederus

Its black wings with contrasting scattered white spots make this a readily recognizable species. The dark reddish brown body is somewhat darker than that of the apparently closely related *P. rufa* Gray and *P. nuptialis* Gerstaecker. These three species have wing coloration unlike that of any other North American species except perhaps *P. americana*. In males of all three, the hypovalves are short and borne on a broad prolongation of the ninth abdominal sternum, and the corresponding ninth tergum is narrowly rounded apically (i.e., not divided into two apical lobes). The females of all three species have thick genital plates without terminal (posterior) lobes (Carpenter, 1931: plate 5, figs. 42-44). These and other characteristics, such as the very elongate seventh and eighth abdominal segments in males, give *lugubris*, *nuptialis* and *rufa* a strong resemblance to certain Mexican Panorpas. It seems likely that these three species entered southern United States from Mexico during a warm interglacial interval, sometime during the Pleistocene.

The known range of *P. lugubris* (Map 1) extends across the Atlantic and Gulf coastal plains from southeastern Virginia through North and South Carolina, Georgia, the northern half of Florida, southern Alabama, southeastern Mississippi, to eastern Louisiana (Livingston Parish, east of Baton Rouge). Carpenter (1935) reported *lugubris* from Dallas, Texas, and from an unspecified locality in New Mexico. Records available to me, however, indicate that the ranges of *lugubris* and *nuptialis* meet but do not overlap (Map 1). Most specimens seen were collected in September through December. There is, however, a smaller spring generation with adults on the wing from mid-April to early June. I have seen a few individuals taken in August and January. Many of the places where *lugubris* has been found have sandy soil and are unshaded or have only a sparse tree cover (cf. *P. rufa*).

Numerous adults of *P. lugubris* were collected in Suwanee Co., Florida, on 6 December 1977. Most of these were preserved at that time, but three males and two females were transported alive to my laboratory at the University of Kansas. Between 9 December and 11 January 1978, these adults were kept in a terrarium for observation of their behavior (GWB rearing lot no. 176). Feeding, mating and oviposition, as well as other behavior, were observed repeatedly during this 37-day period. The males died on 22 and 24 December but presumably had transformed from pupae several days before the females.

During daylight hours, both sexes displayed wing fanning (slow raising of the wings together with spreading them somewhat, then lowering them) and wing flicking (rapid, jerky movements during fanning), frequently accompanied by raising and lowering of the abdomen. Males often struck the venter of abdominal segment 7 against the substrate, and at times they held the hind wings against the sides of the abdomen while fanning the fore wings. Grooming included brushing the wings, chiefly their upper surfaces, and the abdomen with the hind legs, which were then rubbed together. The head and antennae were groomed with the fore legs, followed by rubbing these legs together.

Males did not produce a gelatinous salivary secretion to attract females, as in many other species, but once having fed they vigorously guarded small balls of ground beef provided. When other males approached, a guarding male, standing over the food, would strike laterally with his genital bulb, with the dististyles held widely apart. When a female approached, the guarding male sometimes left the food briefly to grasp the female's abdomen and subsequently bring the genitalia into appropriate position. With the female's body approximately perpendicular to his own and above his back, the male turned his elongate abdomen to one side, bringing the genital bulb nearly 270 degrees around from its initial orientation. The costal margin of the female's wing was clamped in the notal organ, although the wings were held somewhat roof-like above her abdomen but beneath the male's wings. Copulations observed lasted from 6 to 62 minutes, with the female feeding from time to time.

Both the female and the male were usually almost motionless, but the male occasionally fanned his wings. Mating occurred during daylight; after sunset the insects climbed up from two to four inches on clumps of grass or plant stems in the terrarium and rested with vertical orientation (as in *P. nuptialis* and most Mexican species).

Prior to oviposition the female probed in the substrate with her ovipositor, presumably testing for pre-existing cavities, level of soil moisture, etc. Three small dishes of soil about 10 mm. deep were offered for oviposition: sand, sand mixed with humus soil, and humus (such as most other species would use for oviposition). The females laid their eggs only in the humus, not in sand or sandy soil as anticipated. One female was observed to probe and oviposit in the humus, after which she cleaned her ovipositor with her hind legs then went to the dish with sand and humus, probed for a few minutes, and returned to the dish with humus only and resumed ovipository behavior.

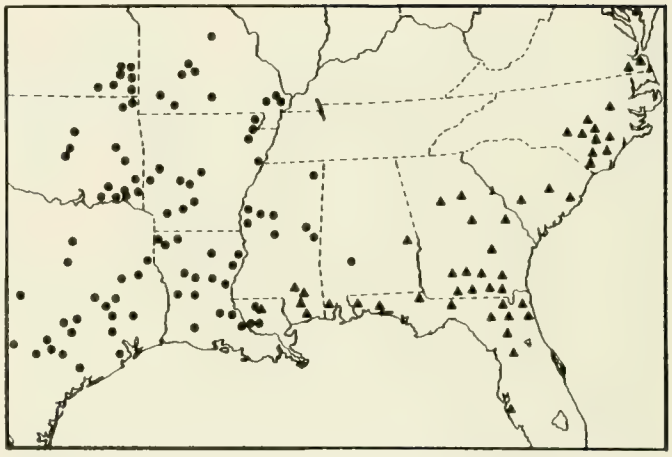
Size of egg clusters and depth of oviposition were variable. Representative clusters contained 12, 18, 34, 35, 37, 37 and 42 eggs and were from 5 to 10 mm. below the soil surface. Mampe and Neunzig (1965: 848) found eggs of *P. lugubris* usually laid singly. Eggs were usually held together by a secretion from the female that was fluid on freshly deposited eggs but which may be the source of an uneven "felt" of matted, fibrous-looking material adhered to the chorion after several hours (in contrast to the smooth chorion of *P. nuptialis* or the "network" of material covering the eggs of several other *Panorpa* species). Pale cream-colored when first laid, the eggs became gray after a few hours, swelled conspicuously to nearly a millimeter in length and eventually darkened to almost black shortly before hatching. Duration of the egg stage was about 7 to 9 days under laboratory conditions.

Upon hatching, larvae were light gray (darker than most first-instar Panorpas I have seen), the head capsule also light gray except for the blackish frons with black egg-tooth and the dark brown mandibles and black eyes. Fed on small nymphs of *Blatella* and on adult *Drosophila* (the preferred food), the larvae grew rapidly, attaining the second instar in four days, the third instar in four more days, and the fourth instar four to five days later. That is, from hatching to beginning of the last larval instar was two weeks or a little less, when abundant food was provided. A week after attaining the fourth instar, larvae reached full size of approximately 17 mm. length (cf. Mampe and Neunzig, 1965: 844) and ate small insects so rapidly that I began feeding them ground beef. By 11 January, many of the larvae had entered pre-pupal diapause (i.e., had ceased feeding and had become quiescent) and the last adult female died; the insects were then preserved and observations discontinued.

The mature larva of *Panorpa lugubris* has been described in detail by Mampe and Neunzig (1965) and by Boese (1973).

Panorpa nuptialis Gerstaecker

Largest and arguably the most colorful North American scorpion-fly, *Panorpa nuptialis* is also the westernmost of our species, if one disregards a couple of questionable records from Utah (Gurney, 1937, 1938) and New Mexico (Carpenter, 1935). It is a common and widespread autumnal species found from southeastern Kansas southward through Oklahoma to southern Texas and eastward to the Mississippi River in Missouri and Arkansas and, farther south, to western Alabama (Map 1). Most collection records are for October, but the species has also been found throughout September and November and, in the southern part of its range, in early December. Carpenter (1931) reported a mid-July occurrence in southeastern Kansas.



Map 1. Geographical distribution of *Panorpa nuptialis* (circles) and *Panorpa lugubris* (triangles). Each symbol represents one or more autumnal collections in a county (or parish, in Louisiana).

Several morphological characters (e.g., the shape of the ninth abdominal tergum, hypovalves of the ninth sternum, shape of dististyles, and relatively elongate abdominal segments in males, and the shape of the genital plates in females) indicate a close relationship of *P. nuptialis* with *P. lugubris*. These same characters suggest a slightly less close relationship of both these species to *P. rufa* Gray. All three (and *P. floridana*, described below) comprise a species group that has many similarities to several Mexican species and that is distinct from other scorpion-flies of eastern United States and Canada.

Habitats in which *P. nuptialis* has been found show that the species is less dependent on moisture than most of its nearctic congeners. I have collected it in grasses in sparse woods and in weedy growth at the edges of woods but also in open grasslands (pastures and even occasionally-mowed roadside grass) and in cultivated fields adjacent to woods (soybeans, cotton, etc.). Unable to find *nuptialis* in apparently suitable habitats on the Mississippi floodplain, I supposed it might have been eradicated there by prolonged use of various insecticides. Other aspects of the habitat of this species, as well as general biology of adults, eggs, larvae and pupae, can be found in an earlier paper (Byers, 1963).

Panorpa rufa Gray

Not a rare species but an elusive one, *P. rufa* is known today—more than 150 years after it was named and described—from only eighteen localities (Map 2). Although I have searched for it at some of these places, in various years, I have never succeeded in finding it. There is a single collection record for 10 May at Southern Pines, North Carolina (Carpenter, 1931), but this is typically an autumnal species, virtually all dates of collection being between the middle of October and 20 December.

All the sites from which *P. rufa* is currently known have sandy or sandy-loam soil, and at least some are characterized by rather sparse longleaf or loblolly pine woods, or a mixture of pine and oak, with grasses the commonest ground cover. (In Bay Co., Florida, for example, the habitat was a plantation of *Pinus clausa* on sand hills.) If one may extrapolate from knowledge of *P. nuptialis* and *P. lugubris*, the other members of the species group to which *rufa* belongs, the insects should be sought late in the day and fairly near the ground, and they are likely to be vertically ori-

ented on slender plant stems, rather than on more horizontal leaf surfaces as in most of our Panorpas.

Panorpa rufa has been found in the following southeastern states and counties on the dates indicated: Alabama, Conecuh Co., 14 Nov.; Lee Co., 20 Oct. and 2 Nov.; Macon Co., 26 Nov.; Mobile Co., 8 Oct. and several dates between 1 and 23 Nov.; Florida, Alachua Co., 21 Oct.; Bay Co., 7 Dec.; Gulf Co., 1 Nov.; Holmes Co., 14 Nov.; Okaloosa Co., 3 Nov.; South Carolina, Clarendon Co., 25 Oct.; North Carolina, Moore Co., various dates from 10 to 20 Oct.; New Hanover Co., 25 Dec. The types are from an unspecified locality in Georgia. Since they were collected prior to 1833, I have put a spot on Map 2 near Savannah, a center of entomological and other cultural activity in the late 18th and early 19th centuries. The published record for Tennessee (Cole and Gillespie, 1950) is omitted from the map because I consider it to be based on a misidentified specimen (a single female, collected in June, in the Great Smoky Mountains). In his study of the Mecoptera of eastern Tennessee, Caron (1967) was unable to find this specimen and also concluded that the record was in error.

See discussion of structural details under *Panorpa floridana*.

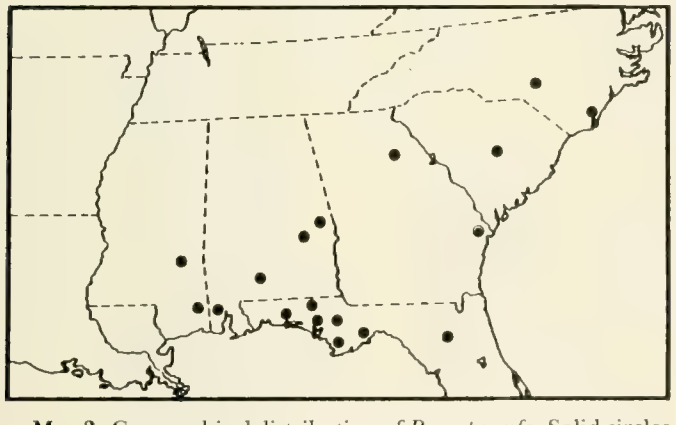
Panorpa floridana new species

Description based on 3 males, 2 females, pinned (terminal segments of one female originally slide-mounted).

Head: Dorsum, frons and rostrum dark yellowish brown to reddish brown; dark brown to black ring around each ocellus. Scape and pedicel dark yellowish brown; flagellum dark blackish brown with 41-45 flagellomeres (41 in left antenna, 45 in right, in holotype).

Thorax: Dorsum dull brown, mostly finely pubescent, with scattered short, black setae, but nearly glabrous and darker brown near bases of wings. Pleural surfaces, mera and coxae dull brown, finely pubescent, with widely scattered pale hairs; these hairs longest and most dense on anterior surfaces of coxae. Legs and tarsi dark yellowish brown except fifth tarsomeres dark brown.

Wings tinged with yellowish brown; bands and spots brown. Apical band diffuse, with broad pale zones bordering all included cross-veins and pale spots in cells slightly before apical margin. Pterostigmal band usually complete (interrupted between M_{1+2} and M_4 in right front wing of male paratype), not branched but with roughly triangular spot at posterior margin near M_4. Marginal spot extending from C to R_{2+3}. Basal band entire but strongly constricted at M. First and second basal spots present, and a conspicuous, more proximal spot in fore wing, from A_1 to A_3. No humeral spots.



Map 2. Geographical distribution of *Panorpa rufa*. Solid circles represent one or more autumnal collections in a county; circle enclosing a spot represents the holotype of this species from an unknown locality in Georgia at an unknown date prior to 1833.

Abdomen of male: Terga 2-5 unevenly dark yellowish brown, corresponding sterna slightly paler. Tergal hairs short, each arising from a small tubercle; hairless, glossy band across most of anterior one-third of terga 3-5. Segments 6-9 darker yellowish brown than more anterior segments, nearly reddish brown. Segments 7 and 8 each slightly longer than 6. Notal organ inconspicuous: a broad, scarcely projecting lobe on posterior margin of tergum 3, with downcurved pale setae, and a small median protuberance with sharp, densely sclerotized tip on tergum 4. Ninth sternum narrowed to slender, median prolongation extending to level of ventral fusion of basistyles (Fig. 3), there dividing into two short, slender branches (hypovalves); hairs short, pale, almost perpendicular to sides of sternal prolongation and hypovalves. Tergum 9 elongate, extending well past ends of basistyles, narrowed to subacute apex; margins thickened on underside and bearing numerous (about 20 on each side) long, thick but pale setae directed mesad, their distal ends crossing in preserved specimens. Basistyles elongate, joined ventrally for slightly more than half their length. Dististyles slender, slightly concave on outer surface in proximal half, abruptly curved in distal one-fourth to acute apex. Inner basal lobe (tooth, of Carpenter, 1931) broadly rounded on posteroventral surface, shallowly concave on concealed anterior surface, with blackened, subacute tooth on dorsal margin.

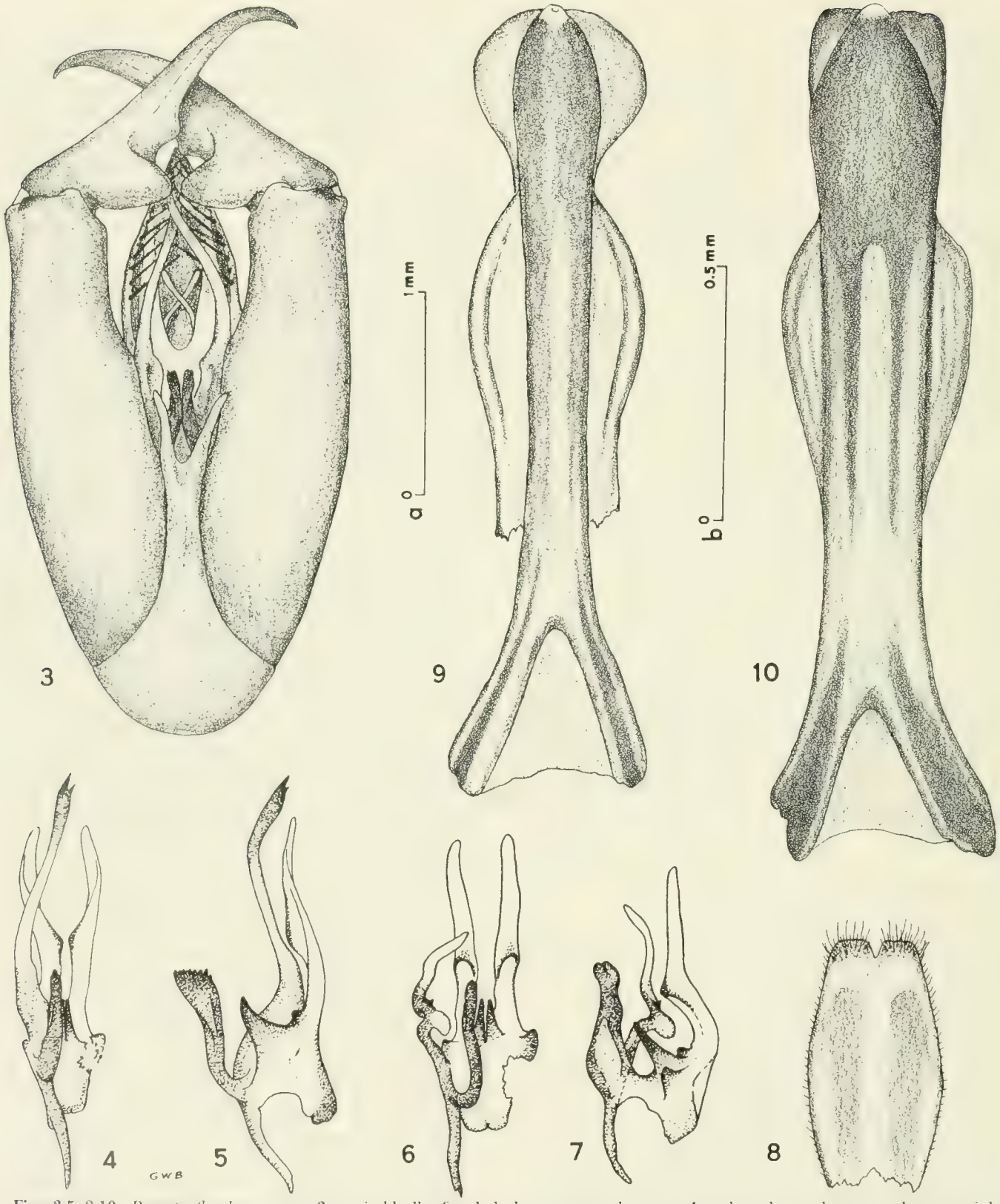
Aedeagus (Figs. 4, 5) with ventral and dorsal valves darkly sclerotized, ventral valves compressed, roughly triangular in lateral aspect; dorsal valves forming a low, median tubercle. Ventral parameres comprising an elongate, smooth dorsal branch with apical and subapical spines and a more densely sclerotized, compressed ventral branch, expanded apically with unevenly serrate margin (seen in lateral aspect) (cf. two-branched hypomere described by Ferris and Rees, 1939, Fig. 51). Dorsal parameres mostly pale, flattened apically, twisted and with darkened mesal edges near mid-length. No aedeagal hamulus. Segments 10 and 11 short, cerci relatively long, slender, crossed in preserved specimens, all concealed beneath ninth tergum but partially visible from below.

Abdomen of female: Terga and sterna dark yellowish brown; cerci black, truncate at apex. Subgenital plate (Fig. 8) with two broad, nearly truncate posterior lobes. Genital plate long, narrow, thick except for small, moderately sclerotized lateral expansions; posterior apex of apical plate blunt or nearly transverse (Figs. 9, 10). Axial portion (mainly spermathecal duct) as wide as dorsal plate posteriorly, with short, thick anterior apodemes connected by thin but hard, sclerotized sheet. Ventral (basal) genital plate apparently absent. Variation in the shape of the genital plate is surprising, especially the rounded to angular sides of the posterior expansions.

Body length, male, about 18.3 to 18.4 mm. (holotype 18.3 mm.). Length of fore wing 13.5 to 13.9 mm. (holotype 13.5 mm.).

Holotype male, Gainesville, Alachua Co., Florida, 10 November 1970, L. A. Hetrick; also labelled "Hort. Unit #2?" and "hammock." Allotype female, and one male paratype, Gold Head Branch State Park, Clay Co., Florida, 20 Nov. 1982, Scott W. Gross. Additional paratypes: male, Orange Park (northern Clay Co.), Florida, 25 Dec. 1936, K. Wheeler No. 8053; female, Alachua Co., Florida, on saw palmetto, 8 Nov. 1974, D. Richman. The holotype is in the Florida State Collection of Arthropods, Gainesville, the allotype is in the USNM, and paratypes are in the SEM and USNM.

Panorpa floridana belongs to what Esben-Petersen (1921) called the *rufa*-group (=*lugubris* group of Carpenter, 1931). It more nearly resembles *P. rufa* than the other included U.S. species, *nuptialis* and *lugubris*. For a time, I considered the few available specimens of this species to be atypical individuals of *P. rufa* because of the striking superficial similarity of the male genital bulb in the two forms and in spite of the dissimilarity in wing coloration. Although there is great variation in wing pattern of *rufa*, it typically has a wide, branched pterostigmal band, often joined posteriorly to the apical band, a large marginal spot, a complete,



Figs. 3-5, 8-10. *Panorpa floridana*, n. sp. **3,** genital bulb of male holotype, ventral aspect. **4,** aedeagal complex, ventral aspect, right ventral paramere removed. **5,** same, right lateral aspect. **8,** subgenital plate, female allotype, ventral aspect. **9,** genital plate, allotype, ventral aspect. **10,** genital plate, female paratype. **Figs. 6, 7.** *Panorpa rufa* Gray. **6,** aedeagal complex, ventral aspect, right ventral paramere removed. **7,** same, right lateral aspect. Scale a, figs. 3-8; scale b, figs. 9-10.

broad basal band continuous with a darkened costal margin connecting the basal band and anterior basal spot. In *rufa*, the background color of the wing is dull, pale yellowish brown, nearly opaque, while in *floridana* it is a translucent brighter yellowish brown. In *floridana* the bands and spots are less extensive than in *rufa* and darker brown. While the genital bulb in *floridana* resembles that of *rufa*, the aedeagus is different in several details, such as the shapes of the branches of the ventral parameres, the dorsal parameres, and the ventral valves. Comparison of figures 4 and 5 (*floridana*) with 6 and 7 (*rufa*, drawn to the same scale and similarly positioned) will make these differences evident. The two-branched ventral parameres of *rufa* are more like those of *P. nuptialis* than those of *floridana* (cf. Ferris and Rees, 1939, Fig. 51, which however depicts the ventral parameres, or hypomeres, of *nuptialis* in an unnatural position, the lower branches in life being close together).

Almost nothing is known of the habitat of this species. The holotype's locality-date information led me to seek additional specimens in 1977 at the Horticultural Unit of the Florida Department of Agriculture. This is at the eastern edge of San Felasco Hammock, northern outskirts of Gainesville. "Hammock" implies a somewhat elevated area surrounded by lower, wetter terrain and characterized by mixed hardwoods. A variety of oaks, red gum, hickory and some pines were noted at the site. The species takes it name from its known geographic range.

Panorpa virginica Banks

This is primarily a species of the middle Atlantic states. I have seen specimens from Virginia, North Carolina, easternmost Tennessee, northeastern Georgia and northwestern South Carolina. Carpenter (1931) recorded it also from northern Georgia, New Jersey and Connecticut. I have not seen the specimen he recorded from Arkansas but feel confident it belongs to the species described here as *P. choctaw*. Similarly, specimens he reported from Michigan and that I reported from Ohio (Byers, 1962a) are *P. hungerfordi* (Byers, 1973).

P. virginica is a late-summer and autumnal species. The holotype, from northern Virginia (Glencarlyn, Arlington Co.), was collected on 10 October. I found a few individuals in Laurens and Chester counties, South Carolina, on 5 Oct. and 16 males, 24 females in Richmond and Johnston counties, North Carolina on 6 and 7 Oct. 1977. Specimens in other collections are from Hoke, Jackson, Johnston, Macon and Wake counties, North Carolina, 12 Sept. to 7 Oct., and Fairfax, Montgomery, Nansemond and Norfolk counties in Virginia, in September. Recently, Wes Bicha has added records from Anderson, Spartanburg, Union and York counties in South Carolina and Banks, Hall and Stephens counties in Georgia, in early to mid-September. There must be a small spring generation in some years; Carpenter's (1931) Georgia record was for DeKalb Co., 2 June, and I have seen a male from Sevier Co., Tennessee, 29 May.

Five species make up what I call the *virginica* group; they are *P. virginica* Banks, *P. neglecta* Carpenter, *P. hungerfordi* Byers and two new species described here — *P. choctaw* and *P. oconee*. *P. hungerfordi* is not a southeastern species and is not considered further, here. (However, the geographical relationship of *hungerfordi* and *neglecta* needs to be examined.) Ranges of the other four, but only in part for *virginica*, are shown on Map 3.

Panorpa neglecta Carpenter

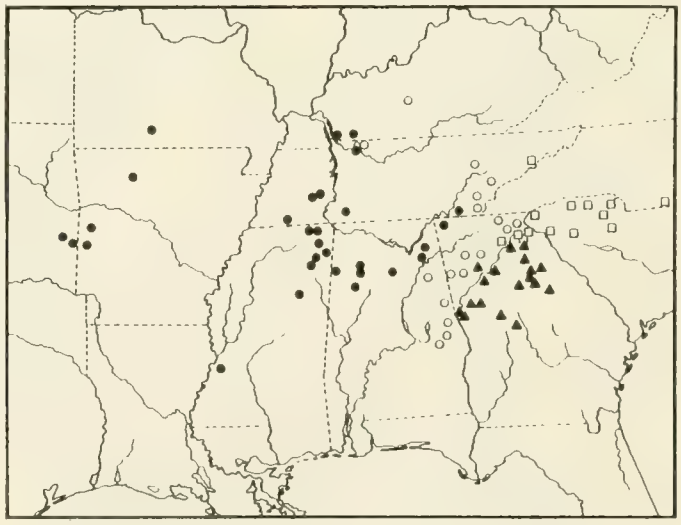
Since it was described, in 1931, this species has been known only from the male holotype, collected at Auburn, Alabama, 19 September 1927, and two specimens from northern Georgia (Carpenter, 1939). With the help of Dr. Kirby Hays, then chairman of the Department of Entomology, Auburn University, I found a suitable habitat near the southwestern edge of the Auburn campus and collected more than 60 specimens, with about equal numbers of males and females.

The habitat was woods-field ecotone of brambles, honeysuckle, greenbriar, and poison ivy at the north edge of a woods, with the brush about one to two feet high. The woods consisted of mostly pine, with some oaks and red gum, small understory trees of dogwood, sassafras, mulberry, etc. Goldenrod was common in the field and ecotone, sparse in the woods (GWB field cat., Alabama, Lee Co. no. 1, 30 September 1977).

Several of the scorpion-flies were engorged with a purplish fluid of which they regurgitated droplets when captured, spotting the net. This fluid's color matched exactly that of the juice of overripe poke berries (*Phytolacca decandra*) that were abundant at the site. Since I could find no living or dead insects other than the scorpion-flies containing this pigment, it is likely that the Panorpas had been feeding directly on the poke berries.

I have not seen the two specimens from Georgia reported by Carpenter in 1939: a male from Blairsville (Union Co.) and a female from Dallas (Paulding Co.). These localities are included on Map 3 since they are consistent with the distribution of *P. neglecta* as otherwise indicated (open circles); however, in my opinion, the "allotype" female was misidentified. The genital plates of the female of *neglecta* are, as anticipated, similar to those of other species in the *virginica* species group, but conspicuously larger (compare Figs. 14, 15, 16). Carpenter's figure 1A (1939: 166) suggests something near *Panorpa helena* (=*venosa* in his 1931 key) or in the *rufescens* species group.

Males from northern Georgia, Tennessee and Kentucky assigned to this species (Map 3) differ from those in eastern Alabama in some details. The ventral, basal rim of the cup of the dististyle is less produced and angular, and the ventral parameres are not as broad at their bases, are slightly longer and have more and larger barbs. In these characters they somewhat resemble males of *P.*



Map 3. Geographical distribution of the *Panorpa virginica* group in southeastern United States. Solid circles - *P. choctaw*; open circles - *P. neglecta*; triangles - *P. oconee*; squares - *P. virginica* (only part of range indicated). Symbols represent one or more collections in a county.

hungerfordi, a northern species from Michigan, Wisconsin, Indiana and Ohio. The geographical ranges as well as the ranges of structural variation in these two nominal species need to be explored further.

Panorpa oconee new species

Description based on 37 males, 28 females pinned, 3 males, 2 females in alcohol.

Head: Dorsum, frons and rostrum including mouthparts dark amber brown; dark brown to blackish spot around ocelli. Scape and pedicel dark yellowish brown, flagellum dark brown to black; 40-43 flagellomeres.

Thorax: Dorsum without distinct markings; pleural surfaces, coxae and mera unevenly yellowish brown (darker in dried, pinned specimens) with fine, silvery pubescence on mesothorax and metathorax, most evident in dorsolateral aspect; scattered pale hairs most dense on anterior surfaces of coxae. Legs dark yellowish brown, tarsi only slightly darker.

Wings strongly tinged with yellow to yellowish brown, with dark brown markings. Apical band complete, broadly concave on proximal side, enclosing small pale spot near end of M or in cell R_{2a} in a few individuals (band complete only to end of M_1 in one male). Pterostigmal band complete, not branched, but with spot near end of M_3. Marginal spot extending from C to R_{2+3} or R_{4+5}. Basal band constricted or broken near mid-length. Basal spot usually from M to Cu_2. Small spot at end of A_2; first humeral spot present but sometimes faint (as in holotype).

Abdomen of male: All terga and sterna unevenly yellowish brown; tergal horn on sixth segment well developed; notal organ consisting of broadly rounded protuberance with downcurved, stiff black hairs on posterior edge of tergum 3 and a median peg-like prominence on tergum 4 covered with black setae curved cephalad. Hypovalves (Fig. 13) extending slightly beyond ends of basistyles, with scattered marginal hairs 3-4 times as long as width of hypovalve, on apical half, and evenly distributed shorter hairs. Tergum 9 (Fig. 12) with U-shaped emargination between two finger-like lobes. Dististyles thick in basal half, narrowing and curving evenly to acute apex. Inner basal cup formed by wide ventral (posterior) flange bearing two prominent, broad, blade-like points, margin between them uneven, darkly sclerotized, and single, broad-based dorsal point (as in Fig. 19). Ventral parameres elongate, reaching apices of dististyles, slightly bowed with tips diverging or less often nearly straight; barbs chiefly on dorsal surfaces of apical two-thirds or more, ventral surfaces smooth, glossy reddish brown; tips acuminate. Dorsal parameres dark brown to black at base, grading through brown to pale yellowish at slightly sclerotized apex, with thin-walled dorsal appendage hanging down toward base of aedeagus. Ventral valves pale, almost membranous, with pale edges diverging from mid-line near base and merging apically with dorsal parameres; dorsal valves apparently fused with bases of dorsal parameres. Aedeagal hamulus flattened, upturned, broadly rounded to nearly truncate at apex, with shallow, median apical notch. Segment 11 recessed within segment 10; long, slender cerci projecting laterad from posterior end of sclerotized, capsule-like segment 10.

Abdomen of female: Terga and sterna yellowish brown in life, sterna slightly paler. In dried specimens, sclerites of segments 1-6 unevenly dark yellowish brown, those of segments 7-11 darker brown; all sclerites pale yellowish brown in specimens preserved in alcohol. Cerci dark brown to black. Subgenital plate pointed at apex, constricted at base by expanded laterotergites. Laterotergites as in *P. choctaw*. Genital plates (Fig. 16) elongate, widest posteriorly, axial portion attaining posterior margin or nearly so, slightly thickened and slightly arched dorsad above basal plate; apodemes about one-third of total length of entire sclerotized structure.

Body length, male, about 10 to 13 mm. (holotype 10.5 mm.); female about 9 to 14 mm. (allotype 11.0 mm). Length of fore wing, male, 12.2 to 13.0 mm. (holotype 12.3 mm.); female, 12.0 to 13.8 mm. (allotype 13.4 mm.).

Holotype male, 2 miles NE of West Point, Troup Co., Georgia, 1 Oct. 1977, George W. Byers. Allotype, 2 miles N of Watkinsville, Oconee Co., Georgia, 3 Oct. 1977, G. W. Byers and H. D. Pratt. Paratypes: GEORGIA: 3m, 3f, same data as holotype; 4m, 6f, same data as allotype; Banks Co., 1 mi. W of Homer, 16 Sept. 1990, WB (1m, 1f); Butts Co., 27 Sept. 1992, WB (1f); Cherokee Co., Woodstock, 5 Nov. 1967, M. Davis (1f); Clarke Co., Athens, North Oconee River, 2 Oct. 1977, GWB (2m, 1f); Athens, 15 Sept. 1980, WB (3m); DeKalb Co., Stone Mt., 1 Oct. 1961, L. Washington (1m); Greene Co., Oconee National Forest, 8 mi. W of Greensboro, 1 Oct. 1977, GWB (4m, 4f); same, but 3 Oct. 1977 (8m, 8f); Gwinnett Co., Loganville, 14 Sept. 1980, WB (8m, 8f); Hall Co., Gillsville, 16 Sept. 1990 WB (2m, 1f); Harris Co., near Pine Mountain, 25 Sept. 1988, WB (1m); Jackson Co., 1 mi. E of Commerce, 16 Sept. 1990 WB (2m, 1f); Lamar Co., 9 Oct. 1982, R. Morris (1m); Meriwether Co., 27 Sept. 1992, WB (1m); Monroe Co., U.S. Hwy 23, 2.7 mi. N of Ga. Hwy. 83, 28 Sept. 1974, T. E. Moore (1m); Monroe Co., 27 Sept. 1992, WB (1m); Morgan Co., 11 mi. W of Madison, 1 Oct. 1977, GWB (1m, 2f); Oconee Co., Oconee Nat. Forest, 15 Sept. 1980, WB (4m, 7f); Watkinsville vic., 16 Sept. and 3 Oct. 1977, C. K. Starr (1m, 1f); Oglethorpe Co., 3 mi. SE of Lexington, 4 Oct. 1977, GWB (2m, 2f); Oglethorpe Co., 1 mi. S of Little Creek, 15 Sept. 1990, WB (2m); Pike Co., 27 Sept. 1992, WB (1m); Taliaferro Co., 2 mi. S of Lyneville, 15 Sept. 1990, WB (1m).

Holotype, allotype, and most paratypes are in the SEM. Other paratypes are in the UMMZ, the Univ. of Georgia and the collection of Wes Bicha, Oliver Springs, Tennessee; paratypes will be deposited in the USNM and the MCZ.

Panorpa oconee is clearly a close relative of *P. choctaw*. Although the two have many characteristics in common, they also show consistent differences, particularly in the genital bulb of the males. Comparison of figures 13 and 17 shows that the ventral parameres of *oconee* are much shorter and more slender than those of *choctaw*, and the projections defining the mesal cup of the dististyle in ventral aspect are shorter and closer together than their counterparts in *choctaw*. The aedeagal hamulus in *oconee* has almost parallel sides enclosing a thin, lightly sclerotized area near the blunt apical margin. Females of *oconee* and *choctaw* are very similar. Those that have been dissected (that is, not identified by association with males) show the axial portion of the genital plates longer in *oconee*, the anterior apodemes longer and the opening of the spermathecal duct nearer to the posteromedian margin (cf. Fig. 16 and Fig. 22).

The small range of *Panorpa oconee* is generally east of those of *P. neglecta* and the more widely distributed *P. choctaw* (Map 3) and southwest of the range of another near relative, *P. virginica*. These four structurally similar species seem to displace each other geographically much as in the case of *Panorpa subfurcata* Westwood, *P. subulifera* Byers, *P. longicornis* Carpenter and *P. carolinensis* Banks.

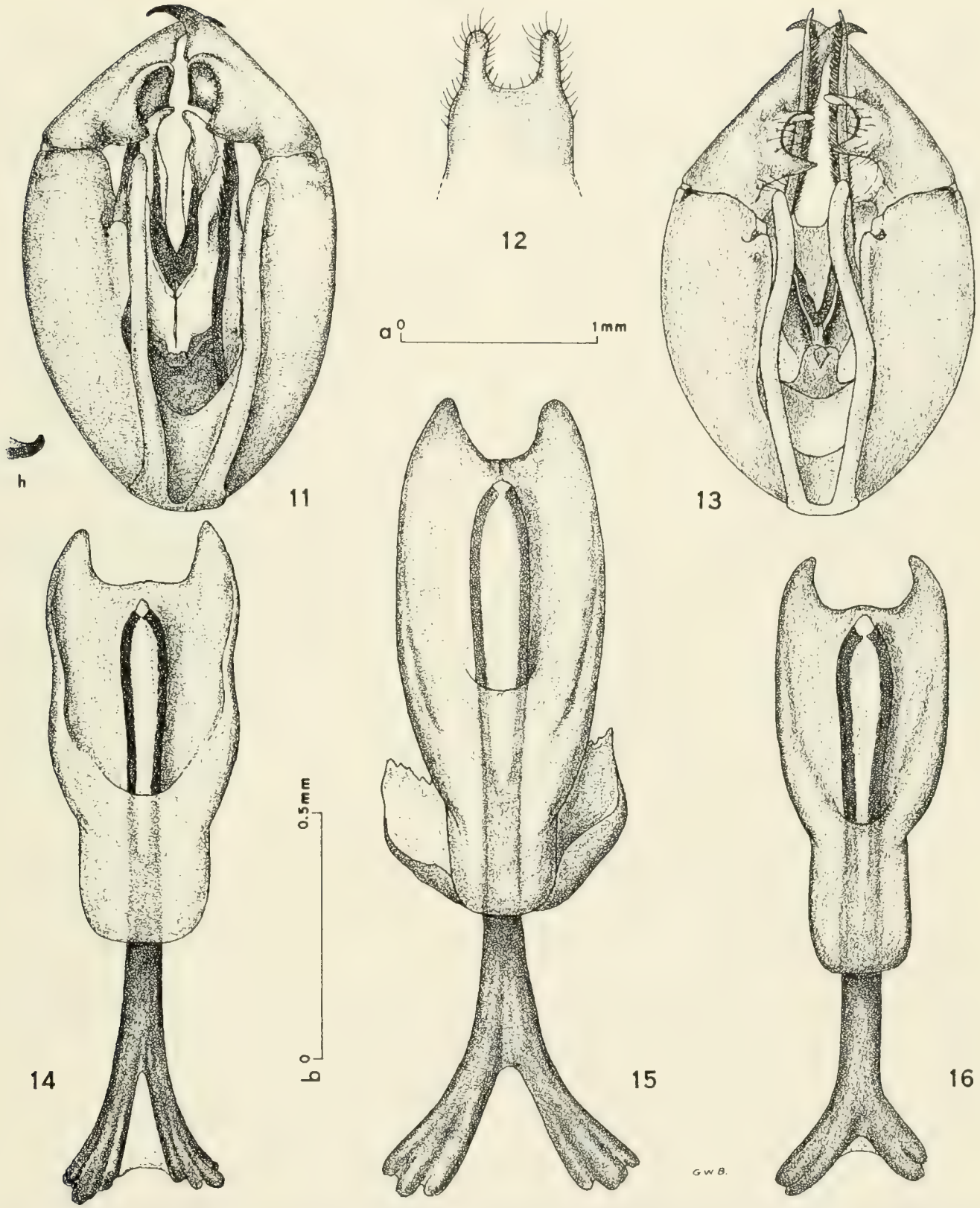
As at the type locality, *Panorpa oconee* has most often been found in association with the tangled growth of honeysuckle, brambles, poison ivy and greenbriars so characteristic of woods borders in the region. The more general environment at the Troup County site was pine woods with saplings of red gum, tulip tree, oaks and juniper. Much of the ground was covered with fallen pine needles.

Panorpa oconee takes its name from some geographical features within its range: the Oconee River, Oconee National Forest and Oconee County, Georgia. The word "Oconee" is of uncertain origin. Possibly derived from a Cherokee word meaning river, it was applied to two divisions of the Creek tribe, according to information supplied by reference librarian Jay Evatt, University of Georgia.

Panorpa choctaw new species

Description based on 107 males, 59 females pinned, 8 males, 9 females preserved in alcohol.

Head: Dorsum of head, frons and rostrum amber-brown, mouth-



Figs. 11, 15. *Panorpa neglecta* Carpenter. **11,** genital bulb, male holotype, ventral aspect; h - aedeagal hamulus, left lateral aspect. **15,** genital plate, topotypic female, ventral aspect. **Fig. 14.** *Panorpa virginica* Banks, genital plate, female. **Figs. 12-13, 16.** *Panorpa oconee*, n. sp. **12,** ninth abdominal tergum, male, dorsal aspect. **13,** genital bulb, male holotype, ventral aspect. **16,** genital plate, female allotype, ventral aspect. Scale a, figs. 11-13; scale b, figs. 14-16.

parts darker brown; irregular dark brown to black pigmentation around ocelli in most individuals. Antennal scape, pedicel and most of first flagellomere amber-brown, rest of flagellum brownish black; 39-41 flagellomeres.

Thorax: Pronotum, mesonotum and metanotum unevenly amber-brown throughout (i.e., no distinct markings). Pleural surfaces, coxae and mera unevenly dark yellowish brown with minute silvery pubescence visible in dorsolateral aspect, and with scattered yellowish hairs most dense on anterior surfaces of coxae. Femora, tibiae and tarsi generally sordid amber-brown, apical tarsomeres dark brown.

Wings strongly tinged with yellow to pale yellowish brown, banded and spotted with dark brown. Apical band complete, its proximal edge usually concave between R_2 and M_1, rarely enclosing small yellowish spots near wing margin; four cross-veins within apical band pale whitish. Pterostigmal band complete, unbranched, extending from proximal half of stigma to apex of Cu_1; outer branch represented by spot of variable extent near tip of M_3. Marginal spot slightly developed, usually extending from C to R_{2+3}, with small spot behind R_{4+5}, less commonly complete from C to behind R_{4+5} or fragmented into small spots. Basal band narrowly constricted or interrupted near mid-length. Basal spot usually extending from M to Cu_2, slightly larger or smaller in some individuals. Small, diffuse spot in angle between tip of A_2 and wing margin. First humeral spot present, second absent (both present in one wing of a female from Oklahoma).

Abdomen of male: Terga and sterna 1-6 sordid yellowish brown, segments 7-9 yellowish brown; conspicuous horn on segment 6; notal organ of tergum 3 only slightly developed, with numerous downwardly curved black hairs. Hypovalves of sternum 9 as long as basistyles or slightly longer, slender, with scattered hairs 3-5 times as long as width of hypovalve on apical half, shorter hairs evenly distributed throughout. Ninth tergum with two short, thick apical lobes (Fig. 18). Dististyles greatly thickened in basal half, with curved, strongly sclerotized, sharply pointed apex. Inner basal cup bordered ventrally by wide flange with irregular, darkened, sclerotized margin bearing large, acutely pointed, blade-like ventral projection (Fig. 17) and more distal, broadly triangular projection (appearing narrow in figure because of ventral aspect). Dorsal side of cup a trapezoidal to broadly triangular flange (Fig. 19). Ventral parameres extending far beyond tips of dististyles as dark reddish brown, smooth blades with acuminate tip and densely set barbs on apical two-thirds or more of dorsal surface. Dorsal parameres black basally, pale yellowish brown apically, with thin dorsal appendage (not visible in ventral aspect). Ventral valves light brown with narrow, pale ridges along ventral margins, ridges in contact at mid-line basally, then diverging and joining apically with dorsal parameres; dorsal valves minute, fused with bases of dorsal parameres; dorsal valves minute, fused with bases of dorsal parameres. Aedeagal hamulus thick, broad, smooth, upturned, with convex lower surface and apex rounded or slightly notched medially. Segments 10 and 11 concealed beneath ninth tergum in dorsal aspect, but elongate one-segmented cerci project laterally, lying against dorsal surfaces of dististyles.

Abdomen of female: Terga yellowish brown in life, somewhat paler in specimens in alcohol, darker brown in dried specimens; corresponding sterna paler than terga; cerci dark brown to black. Subgenital plate approximately elliptical, pointed at apex, constricted by laterotergites at base (Fig. 21). Laterotergites complex, broadest basally (Fig. 20), tapering posteriorly, convex below in life but unevenly concave ventrolaterally when dried; color dark yellowish brown to brown, surface glossy; double fold of thin but sclerotized, paler cuticle at each side immediately below ninth tergum. Genital plates (Fig. 22) elongate, widest posteriorly, with short, wide posterior lobes; axial portion not reaching posterior margin, somewhat widened and slightly arched dorsad above basal plate; apodemes diverging near anterior edge of basal plate.

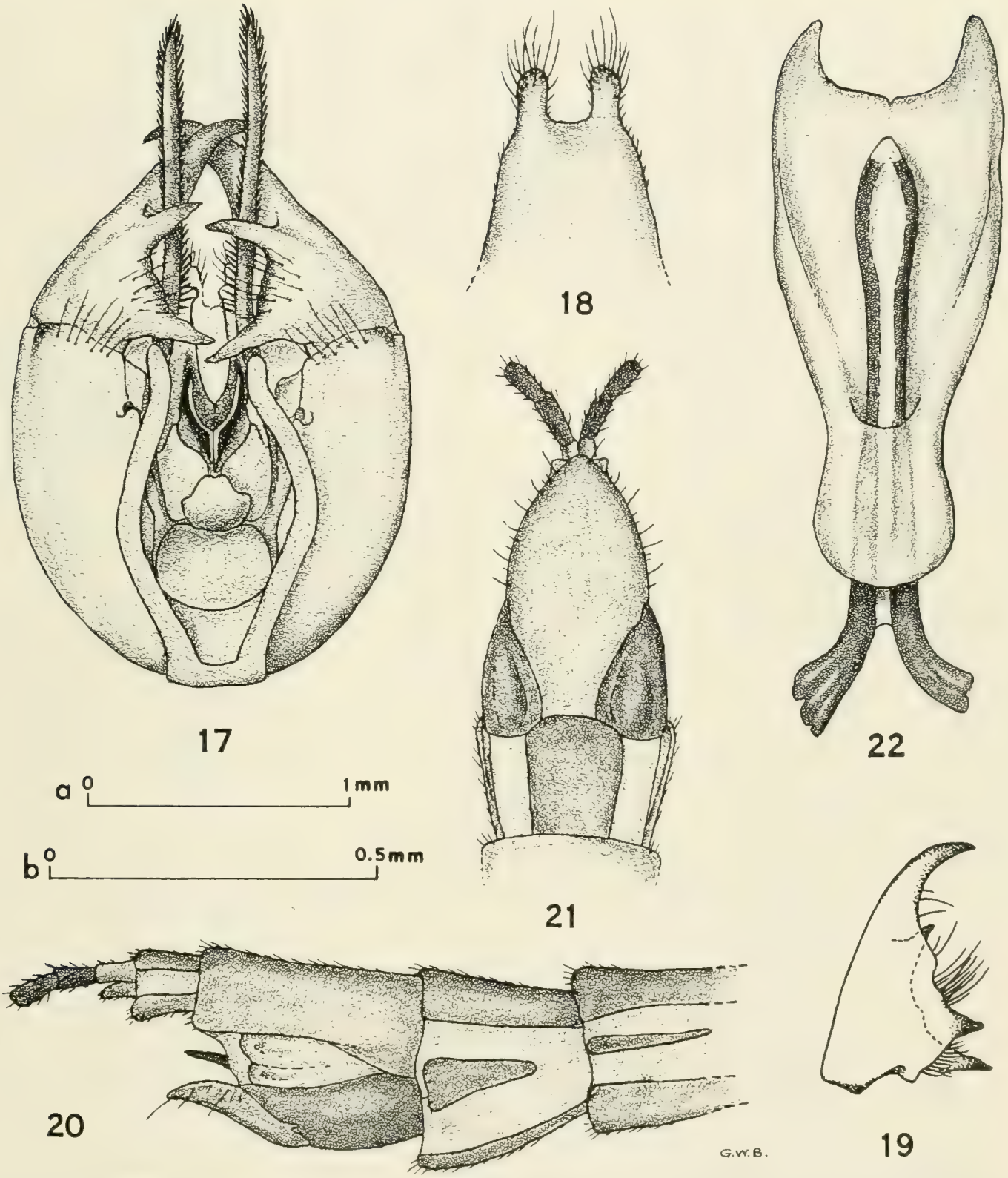
Body length, male, about 10 to 15 mm. (holotype 10.6 mm.); female, also about 10 to 15 mm. (allotype 11.7 mm.). Length of fore wing, male, 10.5 to 14.5 mm. (holotype 11.2 mm.); female, 12.0 to 13.9 mm. (allotype 12.4 mm.). On average, both males and females from the western part of the range (Arkansas and Oklahoma) are slightly larger than those from eastern states.

Holotype, male, Tombigbee State Park, 6 mi. SE of Tupelo, Lee Co., Mississippi, 26 Sept. 1977, George W. Byers. Allotype, 20 male and 18 female paratypes same data as holotype. Additional paratypes: ALABAMA: Blount Co., 13 Sept. 1992, WB (1m); DeKalb Co., Collinsville, 29 Sept. 1988, WB (1m, 1f); Fyffe, 1 Oct. 1988, WB (1m); Etowah Co., 11 mi. W of Gadsden, 13 Sept. 1980, WB (2m, 2f); Fayette Co., 3 mi. W of Berry, 27 Sept. 1977, GWB (1m, 1f); Lawrence Co., Bankhead, 28 Sept. 1975, L. Glenboski (1f); Marion Co., 11 mi. E of Hamilton, 26 Sept. 1977, GWB (2f); Marion Co., 13 Sept. 1992, WB (1m); Winston Co., Corinth Recreation Area, Bankhead National Forest, 27 Sept. 1977, GWB (7m, 3f); Winston Co., Bankhead Nat. Forest, 12 Sept. 1980, WB (6m). ARKANSAS: Newton Co., Dogpatch, 5 Sept. 1971, A. S. Menke (1f); Polk Co., U. S. Hwy. 270 near Scott Co. line, 1160 ft., 27 Sept. 1979, GWB (7m, 8f); Scott Co., Mill Creek at Y City, 740 ft., 27 Sept. 1979, GWB (1m); Ouachita National Forest, T1N, R30W, Sec. 33, 27 Sept. 1979, 1020 ft., GWB (1m, 4f). GEORGIA: Walker Co., LaFayette, 1 Oct. 1988, WB (1m). KENTUCKY: Trigg Co., Land Between the Lakes, 2 Oct. 1982, WB (3m, 1f). MISSISSIPPI: Benton Co., 14 mi. S of Ashland, 7 Sept. 1986, WB (7m); 4 mi. SW of Troy, 21 Sept. 1974, R. Patterson (1m); Chickasaw Co., Davis Lake, 11 mi. WNW of Okolona, 25 Sept. 1977, GWB (3m, 4f); Claiborne Co., Rocky Springs, Natchez Trace Parkway, 14 mi. NE of Port Gibson, 23 Sept. 1977, GWB (3m); milepost 242 Natchez Trace Parkway, 6 Sept. 1986, WB (1m); Itawamba Co., 13 Sept. 1992, WB (1m); Lee Co., Tombigbee State Park, 14 Sept. 1974, R. Patterson (1f); milepost 276 Natchez Trace Parkway, 6 Sept. 1986, WB (3m); Prentiss Co., Boonville, 11 Oct. 1984, S. MacDonald (1f); Tippah Co., 1 mi. S of Falkner, 7 Sept. 1986, WB (2m); Webster Co., 7 mi. W of Walthall, 18 Oct. 1987 (1f), 19 Oct. 1990, T. L. Schiefer (1m). MISSOURI: Douglas Co., 5 Sept. 1981, WB (1m, 1f). OKLAHOMA: Latimer Co., 7 mi. E of Wilburton, 625 ft., 26 Sept. 1979, GWB (1m, 1f); 5 mi. W of Red Oak, 25 Sept. 1977, K. Stephan (1m); locality?, Sept. 1986 (1m, 1f) Sept. 1988 (2m), Sept. 1989 (2m, 3f), Oct. 1988 (6m, 4f), all collected by K. Stephan; Le Flore Co., U. S. Hwy. 270, 3.5 mi. W of Arkansas state line, 27 Sept. 1979, GWB (15m, 11f). TENNESSEE: Bradley Co., 1 Oct. 1988, WB (2m); Chester Co., Chickasaw State Park, 7 Sept. 1986, WB (3m); Hardeman Co., 1 mi. S of Bolivar, 7 Sept. 1986, WB (2m); Henderson Co., 7 Sept. 1986, WB (4m); Wayne Co., mile 347 Natchez Trace Parkway, 5 Sept. 1986, WB (5m).

Holotype, allotype and most paratypes are in the collection of the SEM. Other paratypes are in the collections of Wes Bicha, Oliver Springs, Tennessee; Mississippi State University; Bryant Mather, Clinton, Mississippi; and the Florida State Collection of Arthropods, Gainesville; and paratypes will be placed in the USNM, the MCZ and the the UMMZ.

Panorpa choctaw belongs to a group of species that in many ways resemble *Panorpa virginica* Banks. Males in this *virginica*-group have the basal cup of the dististyle bordered ventrally by a wide flange with a more or less jagged or irregularly toothed margin. They also have long, slender hypovalves, elongate, unbranched ventral parameres and a conspicuous but blunt or rounded aedeagal hamulus. Females are characterized by well developed, sclerotized laterotergites between the ninth abdominal tergum and the subgenital plate and by elongate genital plates the axial portion of which does not reach the posterior margin. The wings in all these species are similarly strongly tinged with yellow to pale amber and marked with dark brown.

Males of *P. choctaw* are readily distinguished from those of other species by the large, blade-like projections from the margin of the basal cup of the dististyle and by the conspicuously elongated, nearly straight ventral parameres that project well beyond the ends of the dististyles. (In males from Arkansas and Oklahoma, the ventral parameres are somewhat shorter than in males from east of the Mis-



Figs. 17-22. *Panorpa choctaw*, n. sp. **17,** genital bulb, male holotype, ventral aspect. **18,** ninth abdominal tergum, male paratype, dorsal aspect. **19,** right dististyle, male paratype, dorsal aspect. **20,** terminal abdominal segments, female allotype, right lateral aspect. **21,** same, ventral aspect. **22,** genital plate, female allotype, ventral aspect. Scale a, figs. 17-21; scale b, fig. 22.

sissippi River, and the distal margin of the cup of the dististyle is less conspicuously projecting.) Females may be recognized by the greatly developed and complex laterotergites of the ninth abdominal segment (but see *P. oconee*).

Adults of this species occur on shaded, low vegetation primarily at the edges of woods. At the type locality, they were on the regionally typical ecotone vegetation of brambles, greenbriars, honeysuckle and poison ivy at the edge of a woods of red oak, white oak, sweet gum, some pine, etc., with a sparse understory of dogwood, sassafras and other species. The flight period of *P. choctaw*, as far as now known, is from 5 September to 2 October, with a distinct peak in late September.

This species is named for the Choctaw Indians, who at various times inhabited the lower Mississippi region and migrated as far east as Georgia, then were forced to move westward into eastern Oklahoma. Lands occupied by the Choctaws correspond approximately to the range of *Panorpa choctaw*.

Panorpa bichai new species

Description based on 21 males, 2 females in alcohol, 6 males, 1 female pinned (most originally preserved in alcohol).

Head: Dorsum, frons and rostrum light amber-brown, apex of rostrum and mouthparts darker brown; irregular black spot around ocelli. Antennal scape pale yellowish brown, pedicel and basal one or two flagellomeres gray, grading into black on most of flagellum; 37-41 flagellomeres but 37 or 38 in most individuals.

Thorax: Pronotum, mesonotum and metanotum yellowish brown without darker markings. Pleural surfaces and coxae pale yellowish brown, with four small but conspicuous black spots, one at anteroventral and posterodorsal corners of mesepimeron and metepimeron (less conspicuous in dried specimens). Femora pale brown, tibiae and tarsi slightly darker, appearing grayish because of rings of slender black setae.

Wings tinged with yellow, banded with dark brown. Apical band complete or, more often, fragmented into spots or with included pale areas; enclosed cross-veins white. Pterostigmal band diagonal from proximal half of stigma to near end of Cu_1, narrowed near its mid-length and with uneven edges; distal branch represented by small spot near margin between M_3 and M_4. Marginal spot present, variable in size. Basal band constricted near mid-length or divided into two spots. Basal (first basal) spot variable in extent from Rs to Cu_2 or smaller. Humeral spots absent.

Abdomen of male: Terga 2-5 unevenly grayish brown dorsally, yellowish brown at sides; corresponding sterna pale yellowish brown; segments 6-9 darker yellowish brown; conspicuous horn on segment 6; notal organ a low, broad lobe on posterior margin of tergum 3 bearing downwardly curved black hairs and a small, forwardly curved peg on tergum 4. Hypovalves of sternum 9 extending approximately to ends of basistyles (Fig. 23), of uniform width throughout, with yellowish hairs longer than width of hypovalve along mesal edges, shorter hairs along outer edges. Lobes of tergum 9 rounded apically; tergum slightly narrowed before bases of lobes (Fig. 24). Dististyles (Fig. 23) with outer margins shallowly concave near mid-length, apical one-third densely sclerotized, curved inward and sharply pointed. Inner basal cup shallow with darkly sclerotized margins. Thick, black setae (usually 3) on inner, apical protuberance of basistyle (Figs. 23, 25). Ventral parameres long, slender, extending well beyond ends of basistyles, their outer ends often bent dorsad, mesad or both; lateral (outer) edge of each densely sclerotized, smooth, with sparse hairs on apical half; inner edge pale with fringe of flattened, dark reddish brown barbs along almost entire length, terminating in apical spine (Fig. 26). Dorsal parameres black mesally near base, pale apically with membranous dorsal appendage. Ventral and dorsal valves of aedeagus not clearly differentiated. Aedeagal hamulus (Fig. 23) conspicuous, with two elongate, attenuate, flattened tines extending beyond bases of dorsal parameres. Segments 10 and 11 mostly concealed by ninth tergum; apical halves of cerci visible in dorsal aspect.

Abdomen of female: Terga unevenly yellowish brown, sterna slightly paler than terga; cerci black. Subgenital plate widest near base, obtusely pointed at apex, medially membranous at base, with wide apical margin pale, subhyaline (Fig. 27). Genital plates (Figs. 28, 29) with thick anterior apodemes, axial portion not attaining posterior margin of distal plate; apical projections of distal plate slightly curved mesad; thin, sclerotized calyx attached to basal plate, curving loosely around distal plate to connect to sides and roof of genital chamber.

Body length, male, 11.2 to 14.6 mm (holotype, pinned, 11.8 mm); female, 9.4 to 11.2 mm (allotype, pinned, 9.4 mm). Length of fore wing, male, 10.0 to 12.1 mm (holotype 10.6 mm); female, 12.2 to 12.3 mm (allotype 12.3 mm).

Holotype male, Frozen Head State Park, Morgan Co., Tennessee, 5 August 1989, collected by Wes Bicha. Allotype, 13 male and 1 female paratypes, same data as holotype. Additional paratypes: TENNESSEE, Anderson Co., 12 August 1989, WB (8m); Anderson Co., Department of Energy Reservation, 10 Sept. 1990, WB (1m); Fentress Co., 10 Sept. 1990, WB (2m); Hawkins Co., Laurel Run, 1200 ft., 12 mi. W (label says E) of Kingsport, 14 Aug. 1982, H. D. Baggett (1m); Morgan Co., Frozen Head State Park, 12 Sept. 1988, WB (1m). Holotype, allotype and 4 paratypes in the SEM. Paratypes in collections of WB, USNM, and the Florida State Collection of Arthropods, Gainesville.

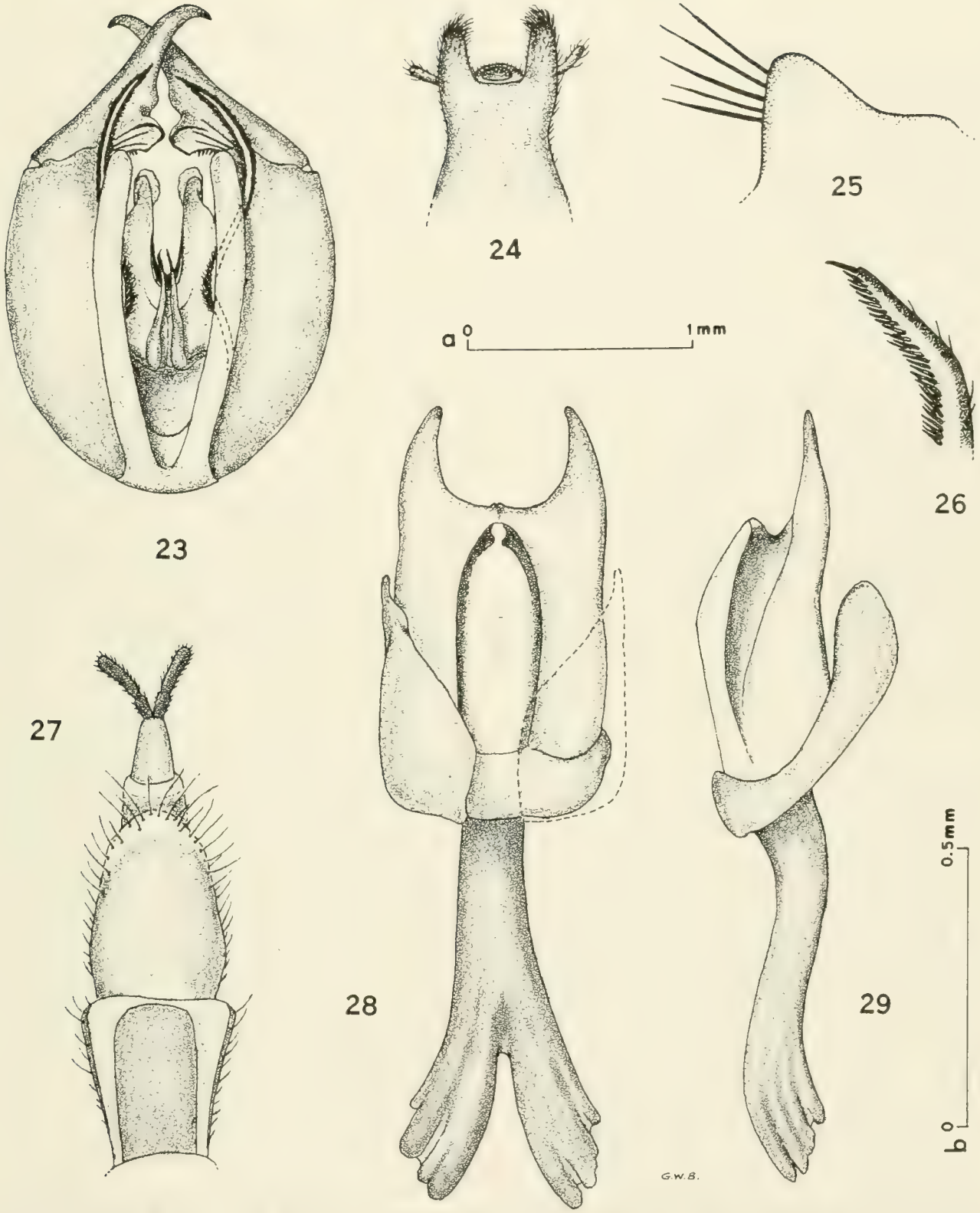
This species is named for Mr. Wesley (Wes) Bicha, engineer and amateur entomologist, who collected nearly all the specimens and who has made the geographic ranges of many nearctic Mecoptera better known, as a result of his extensive travels and enthusiastic collecting.

Panorpa bichai most closely resembles *P. setifera* Webb, and both these species have numerous structural similarities to *P. debilis* Westwood. At the time Webb described *setifera*, both he and I were impressed by its resemblance to *P. helena* Byers in wing pattern and presence of thick, black setae on ventro-mesal prominences on the basistyles of the male. However, I now think that the aedeagal hamulus is a stronger indication of relationship. This structure and the wing pattern of *bichai* and *setifera* agree even more closely with these characters in *debilis* than in *helena*. The apical setae on the basistyles are thickened in *bichai* (Figs. 23, 25) and *setifera*, as in *helena*, but are borne on a prominence as in *debilis*, not as in *helena*.

The most conspicuous difference between males of *P. bichai* and *P. setifera* is in the ventral parameres. These are only slightly curved, and much broader in the basal part (at the level of the aedeagal hamulus) than in the apical half, in *setifera*, and extend only slightly beyond the apex of the aedeagus or the basistyles. In *bichai* they are bowed outward, are more slender throughout and extend far beyond the ends of the basistyles (Fig. 23).

Panorpa bifida Carpenter

Both the geographic and seasonal distributions of *P. bifida* remain sketchy. Described from western Pennsylvania, the species was subsequently found in Champaign and Ross counties, Ohio, and Tyler Co., West Virginia, near the Ohio River. I have collected it from time to time in Giles Co., Virginia (14 June 1975, 2 and 8 July 1975, 23 July 1979, 11 Aug. 1982, 5 July 1986 and 25 July 1992, at elevations from 554m. to 1060 m.), where it has always been uncommon. And Wes Bicha has found it at Lobelville, Perry Co., Tennessee, on 5 Sept. 1986 and 22 Sept. 1991. The last of these records shows that *bifida* can be autumnal in occurrence, although it is primarily a mid-summer species.



Figs. 23-29. *Panorpa bichai*, n. sp. **23,** genital bulb, male paratype (topotypic), ventral aspect; dashed line indicates shape of ventral paramere. **24,** ninth abdominal tergum, dorsal aspect. **25,** ventro-mesal apex of right basistyle, male holotype. **26,** apex of right ventral paramere, holotype. **27,** terminal abdominal segments, female allotype, ventral aspect. **28,** genital plate, female allotype, ventral aspect; dashed line indicates cuticular fold partially enveloping basal and apical plates. **29,** same, right lateral aspect. Scale a, figs. 23-24, 27; scale b, figs. 25-26, 28-29.

Panorpa braueri Carpenter

Three males and five females of this uncommonly collected species were found in a narrow, shaded ravine near the western edge of Bentonville, Benton Co., Arkansas, on 21 Sept. 1977, and one male, two females were collected at the same site on 28 Sept. 1979. The scorpion-flies were on herbaceous plants (mainly mints) beside the dry bed of a small brook, shaded by white oak, sycamore, elm and other deciduous trees. The type series (1m, 3f) was collected in adjacent Washington County, in May; and there are September records from this county. The species is known also from Marion Co., Arkansas, and Carter, Barry, Franklin, Gasconade, Green, Laclede, Newton and Pulaski counties in Missouri, in May-July.

Panorpa isolata Carpenter

Although for some time it has appeared that this species is bivoltine with peaks of emergence in June and August (Byers, 1954), it is also autumnal in the southeastern states. Following are examples: Georgia, Clarke Co., 20 Oct. 1973 (1m); Franklin Co., 11 Nov. 1974 (1f); Gwinnett Co., 1 Nov. (year not recorded) (1f with anterior basal spot and humeral spots fused in left front wing); Alabama, Calhoun Co., 21 Sept. 1966 (1m).

Based on his extensive collecting experience, Wes Bicha considers *P. isolata* to be bivoltine in the Southeast, with peaks of emergence in early May and again in August until mid-September, and with some individuals present until frost.

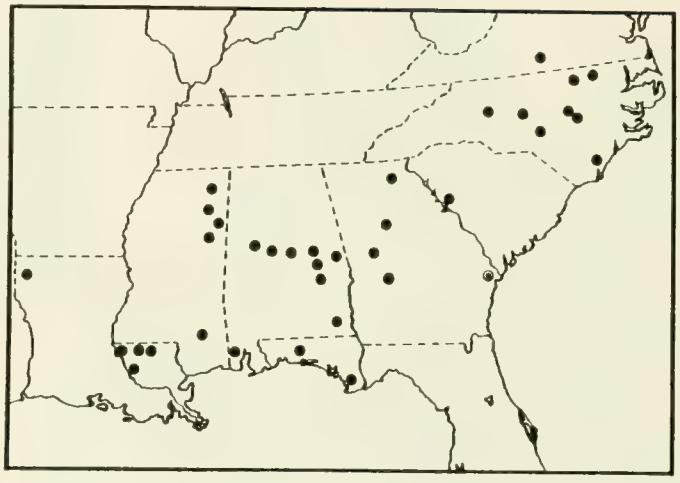
P. isolata has been found in Mississippi (Yalobusha Co., Tishomingo Co., May records only), Alabama, Georgia, eastern Tennessee, western North and South Carolina and the District of Columbia. Carpenter (1935) also recorded it from Waukegan, Illinois; but I think he must have confused it with his *Panorpa dubitans*, the key difference between males of the two being a slight difference in length of hypovalves.

Panorpa americana Swederus

Chiefly a lowland species, *P. americana* has been found from New Jersey and Delaware southwestward across Virginia, the Carolinas, Georgia, northern Florida, Alabama and Mississippi to Louisiana (Map 4). It is clear from this map of collecting localities, however, that our knowledge of the range of *americana* is fragmentary and uneven. The collections I have seen also suggest that *P. americana* is never an abundant species where it has been found. Most of these places are less than 150 m. above sea level, and all but one are below 300 m. (about 1000 ft.). The exception (Carpenter, 1939) is Yonah Mountain, Georgia (in White County), the base of which is near 450 m., the summit 850 m. Inclusive dates for this collection of 4 specimens are 10-20 June, also exceptional, as all other records are for late September to early November.

P. americana is an easily recognized species, its relatively broad wings deeply tinged with yellow, the dark brown apical, pterostigmal and basal bands with fairly even edges, the marginal spot small and the anterior basal spot merged with a single (first?) humeral spot.

Nothing has been published regarding the habitat of *P. americana*. My collections in the fall of 1977 indicate that in much of the southern part of its range this species occurs in woods-field ecotones shared with various other Panorpas. In Oktibbeha Co., Mississippi (near State College, 25 September), *americana* was found on honeysuckle (*Lonicera* sp.) only a little above ground level.



Map 4. Geographical distribution of *Panorpa americana*. Solid circles represent one or more autumnal collections in a county (or parish, in Louisiana); circle enclosing a spot represents the holotype of this species from an unknown locality in Georgia at an unknown date prior to 1787.

In Chickasaw Co., Miss. (near Woodland, 25 Sept.), the habitat was brambles (*Rubus* sp.), honeysuckle, greenbriar and poison ivy. In Elmore Co., Alabama (6 mi. W of Wetumka, 29 Sept.), it was brambles and honeysuckle. And in McCormick Co., South Carolina (Sumter National Forest, near the Savannah River, 4 October), *americana* was again found on honeysuckle, greenbriar, brambles and trumpet vine (*Campsis radicans*). In each of these localities, a variety of habitats was investigated.

Panorpa gracilis Carpenter

Only two males comprised the type series of this species (Carpenter, 1931). These were collected at or near Tarboro, North Carolina, in April and May 1924. The species was not found again until 1977. It seemed to me that *gracilis* might also have an autumnal flight period, and being in the Tarboro vicinity on 8 October, I drove there in search of *P. gracilis*. In early afternoon, I stopped at a woods about 2 miles east of Tarboro on U. S. Highway 258. There, on the narrow floodplain of a tributary of the Tar River, I found, in two hours of collecting, a few individuals of *Panorpa virginica* and more than 70 males and females of the elusive *P. gracilis*.

The habitat was shaded by oaks, hickory and, near the small, clear, sand-bottomed stream, sycamore, red gum and bald cypress (with "knees," suggesting prolonged spring flooding). Ground cover was mainly poison ivy and greenbriar. *Panorpa gracilis* was found most often on patches of *Tradescantia* growing together with *Carex*, nettles and greenbriars near the bases of cypress trees (GWB field cat., North Carolina, Edgecombe Co. no. 1).

Later the same day (8 Oct.), I collected two males and six females of *gracilis* 11 miles southeast of Enfield, Halifax Co., North Carolina.

More recently the known range of this species has been considerably extended by the collecting activities of Wes Bicha, as follows: NORTH CAROLINA: Beaufort Co., 7 May (3m, 1f) and 17 Sept. 1980 (3m, 3f); Edgecombe Co., 6 May 1980 (8m, 3f), 14 June 1990 (1m, 3f); Martin Co., 7 May 1980 (2m, 1f); Perquimans Co., 18 Sept. 1980 (2m, 1f); and Pitt Co., 3 June 1990 (1m). VIRGINIA: Chesterfield Co., 12 June 1981 (1m, 1f); Greensville Co., 7 May 1980 (no count); Sussex Co., 12 June 1981 (1m, 1f).

Panorpa gracilis is a vigorous "tumbler," rolling over and over in the net, or dropping readily to the ground when only slightly disturbed. When approached, the insects fly a few inches to a few feet, as most Panorpas, but if alarmed again they fly a short distance, land on a leaf and tumble over the edge to the ground (not to the underside of the leaf).

When he described *P. gracilis*, Carpenter (1931) recognized its structural similarity to *P. interrupta* Banks (now *P. banksiana* Penny and Byers). It is even more similar to *P. palustris* Byers (1958), but this similarity did not occur to me in 1958 because the ventral parameres of *gracilis* were originally described as without barbs. Subsequent examination of the holotype of *gracilis* (Fig. 31) revealed that these parameres do indeed have barbs on the inner, basal 80 per cent of their length, while approximately the apical 20 per cent is bare. In a few pinned males of *gracilis*, one or both ventral parameres are twisted into a position that makes the barbs primarily dorsal and thus not immediately seen in ventral aspect. In *P. banksiana* (Fig. 30), the ventral parameres (which Carpenter, p. 248, inadvertently called hypovalves) are much longer than in *gracilis*, extending far up between the dististyles, and are greatly thickened in their basal two-thirds and essentially bare (i.e., without barbs). See also *P. palustris*.

Since the female of *P. gracilis* has been unknown, the subgenital plate and the genital plates are illustrated here (Figs. 36, 38, 39). Absence of apodemes projecting cephalad from the basal plate is striking, as is also the similarity of the genital plates of *gracilis* to those of *P. palustris* (Figs. 40, 41).

Panorpa palustris Byers

This species is included because of its geographic range; the available dates of its collection are not truly autumnal. It was originally found in mid-September, in southeastern Virginia, at the western edge of the Great Dismal Swamp, then in Nansemond Co., now Suffolk. Subsequently it was collected near Virginia Beach in early September, and more recently in nearby Camden Co., North Carolina, on 18 Sept. 1980 (WB). There are spring and summer records for Caroline, James and Spotsylvania counties in Virginia.

In the form of the dististyles, hypovalves and aedeagus, males of *P. palustris* rather closely resemble those of three other regional species: *gracilis* Carpenter, *dissimilis* Carpenter and *banksiana* Penny and Byers (formerly *interrupta* Banks). Since in all four species the inner basal cup of the dististyle is more or less ventral in position so that its shape can readily be determined, I have illustrated dististyles of all four, side by side, for comparison and identification purposes (Figs. 32-35). This concavity on the dististyle is narrow and shallow in *palustris* (Fig. 35) and is divided by a thin diagonal carina. In preserved specimens, the ends of the ventral parameres usually lie in the groove along the basal side of this carina. There is only a slight indication of such a carina in *dissimilis* (Fig. 33), and the irregular outer, ventral margin of the cup is conspicuously more protruding than in *palustris*, although this curved, ridge-like structure is variable in both species. In *banksiana* and *gracilis* there is no carina, the shape of the cup differs especially in width, and the darkened point on the dorsal margin is more basal in *banksiana*. As pointed out earlier, under *P. gracilis*, the ventral parameres of *banksiana* and *gracilis* are completely different; they are more similar in *palustris* and *dissimilis*.

The female of *P. palustris* has not been described heretofore. Taxonomically useful details are therefore illustrated in Figures 37, 40 and 41.

Panorpa banksiana Penny and Byers

Originally named *Panorpa interrupta* by Banks (1918), this species was re-named (Penny and Byers, 1979) because of its secondary homonymy with *P. interrupta* (Navás, 1913, described as *Aulops* and now a synonym of *P. japonica*). Banks' syntypes are labelled "Raleigh, N.C., Late Sept. 1915, F. Sherman."

Spring records for *banksiana* are more numerous than autumnal ones. There are autumnal collections from the vicinity of Raleigh (Wake Co.), North Carolina, from 23 to 27 September and on 17 October, and from Harnett Co., 27 Sept., Lee Co., 16 Sept., and Duplin Co., 4 Oct., all in North Carolina. Spring records include also Ashe, Henderson, Johnston, Nash, Robeson and Wilson counties, from April to June.

In aedeagal structure and form of the dististyles (Fig. 30), this species belongs to a group together with *P. gracilis*, *P. palustris* and *P. dissimilis*. See discussion of *P. gracilis*.

Panorpa hispida new species

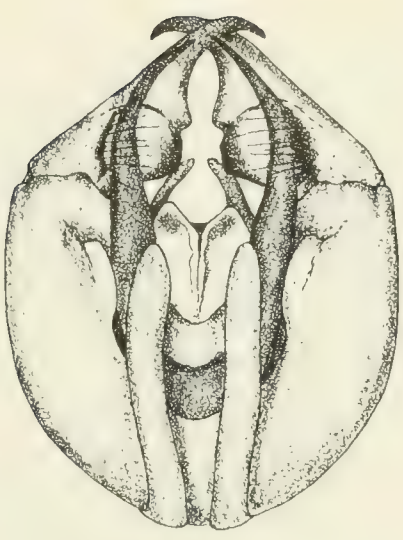
Description based on 26 males, nine females, pinned from alcohol.

Head: Dorsum, frons and rostrum glossy dark yellowish brown, with black ring around base of each ocellus. Maxillary and labial palps yellowish brown except apical one-third to half of each terminal segment dark brown to black. Scape, pedicel and proximal half of first flagellomere yellowish brown, rest of flagellum brownish black; 36-38 flagellomeres (36 in holotype, 38 in allotype).

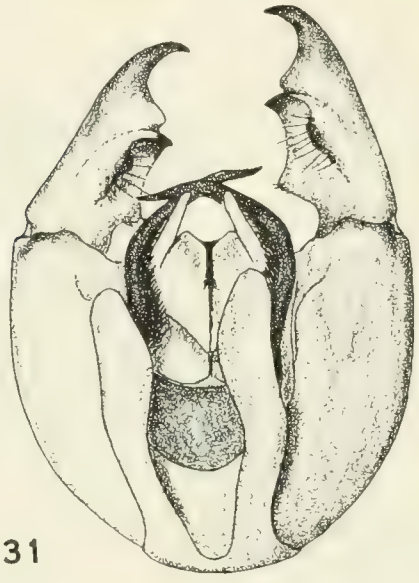
Thorax: Dorsum evenly light brown, without any pattern of markings; pleural surfaces, coxae and mera dull yellowish brown with sparse yellowish hairs and some darker, longer hairs on anterior surfaces of coxae. Legs dull yellowish brown, with scattered black spines on tibiae; tarsi darkening from dark yellowish brown on basitarsus to almost black on apical tarsomere; terminal ring of black spines on first four tarsomeres.

Wings tinged with yellow to light yellowish brown, bands and spots dark brown. Stigma whitish in specimens mounted from alcohol. Apical band with two or three included pale spots. Pterostigmal band complete but not branched, its distal branch represented by dark spot at margin between M_3 and M_4. Marginal spot small, from C to slightly behind R_1. Basal band interrupted near midlength, anterior part extending from C to M, posterior part from slightly before Cu_1 to wing margin. First basal spot and first humeral spot present.

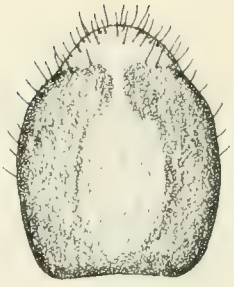
Abdomen of male: Terga 1-5 unevenly sordid yellowish brown, corresponding sterna paler yellowish brown; sixth segment more uniformly dark yellowish brown, with tergal horn; notal organ only weakly developed, downcurved hairs on posterior edge of tergum 3 slightly darkened and thickened. Genital bulb (Fig. 42) wider than length measured to ends of basistyles. Hypovalves slender, of nearly uniform width throughout but narrowing slightly in apical one-third, with long, slender, dark setae along mesal margins. Inner, ventral apex of each basistyle bearing 2-3 long, thick, black setae, usually divergent from their bases (Fig. 42). Tergum 9 (Fig. 45) with posterior lobes slender, about three times as long as wide, and bearing dark apical setae. Basal cup of dististyle shallow, its inner surface nearly flat, with ventral (posterior) and apical margins strongly sclerotized and slightly darkened; about ten short, black setae along dorsal margin (Fig. 44). Apical one-third of dististyle bent somewhat dorsad, curving evenly to darkened, acute tip. Ventral parameres (Fig. 43) curved dorsad and mesad, densely sclerotized, with barbs along inner margin increasing in length toward apex of paramere. Dorsal parameres slightly darkened at base, pale yellowish at apex, with nearly transparent dorsal appendage hanging down and concealed in ventral aspect. Ventral valves pale, their ventral edges diverging from midline and merging apically with dorsal parameres; dorsal valves inconspicuous, light brown but strongly sclerotized, merging dorsally with black bases



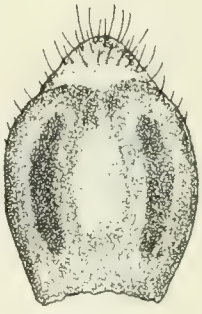
30



31



36



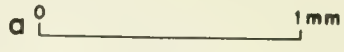
37

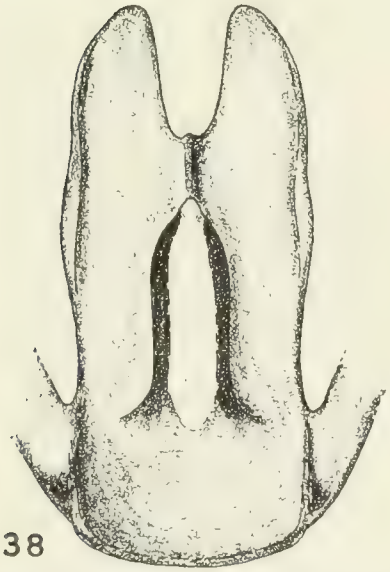
32

33

34

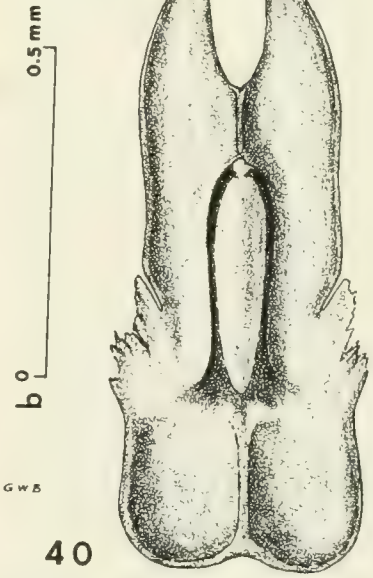
35





38

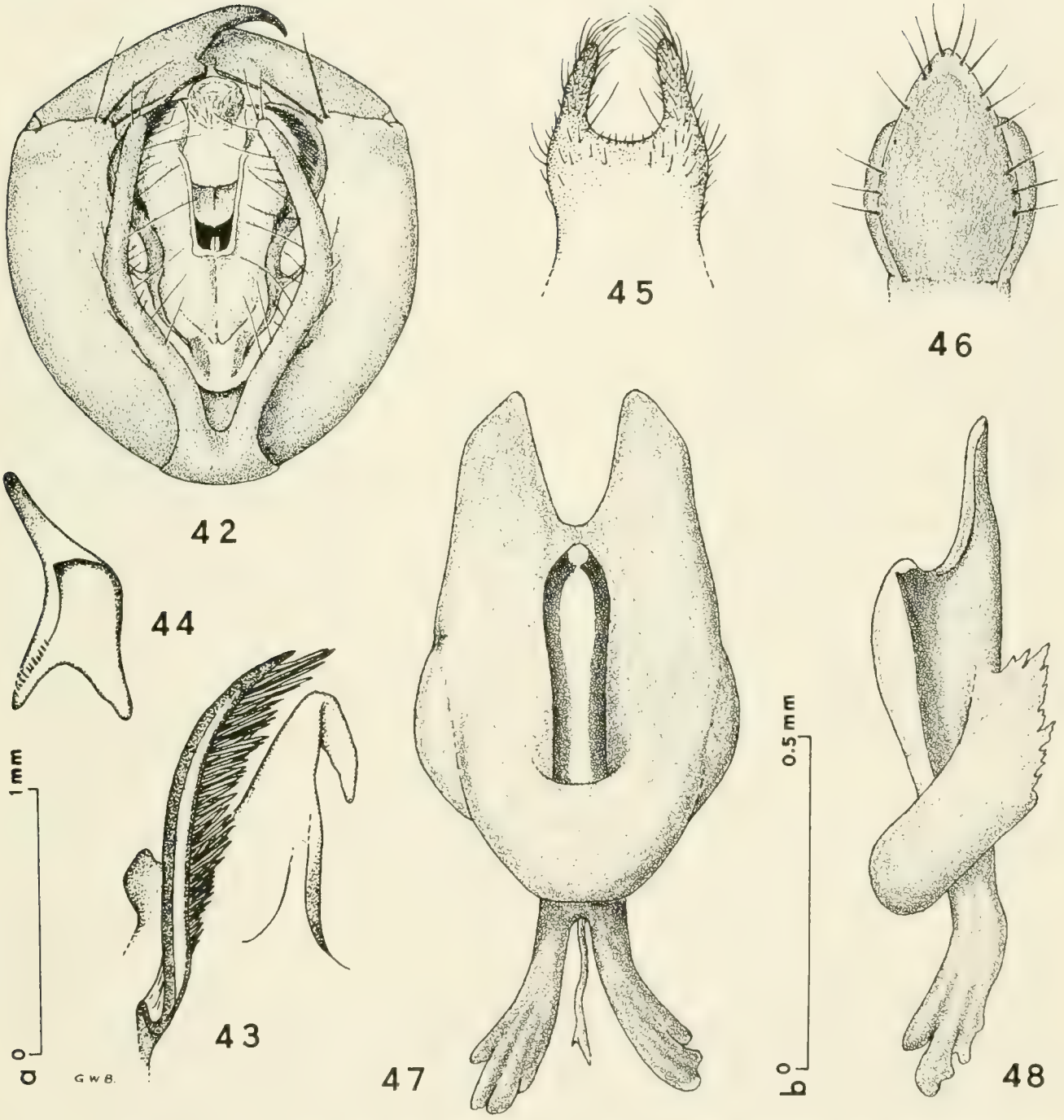
39



40

41

Fig. 30. *Panorpa banksiana* Penny and Byers, genital bulb, male holotype (of *P. interrupta* Banks), ventral aspect. **Figs. 31, 36, 38-39.** *Panorpa gracilis* Carpenter. **31,** genital bulb, male holotype, ventral aspect. **36,** subgenital plate, female, ventral aspect. **38,** genital plate, female, ventral aspect. **39,** same, right lateral aspect. **Figs. 32-35.** *Panorpa* species, left dististyles of males, ventral aspect. **32,** *P. banksiana.* **33,** *P. dissimilis.* **34,** *P. gracilis.* **35,** *P. palustris.* **Figs. 37, 40-41.** *Panorpa palustris* Byers. **37,** subgenital plate, female, ventral aspect. **40,** genital plate, female, ventral aspect. **41,** same, right lateral aspect. Scale a, figs. 30-37; scale b, figs. 38-41.



Figs. 42-48. *Panorpa hispida*, n. sp. **42,** genital bulb, male paratype, ventral aspect. **43,** left ventral and dorsal parameres, ventromesal aspect (making breadth and curvature of ventral paramere less obvious). **44,** right dististyle, mesal aspect. **45,** ninth abdominal tergum, male paratype. **46,** subgenital plate, female allotype, ventral aspect. **47,** genital plate, allotype, ventral aspect. **48,** same, right lateral aspect. Scale a, figs. 42, 44-46; scale b, figs. 43, 47-48.

of dorsal parameres. No aedeagal hamulus. Apex of segment 11 lying between dorsal parameres in most specimens.

Abdomen of female: Both terga and sterna sordid yellowish brown, sterna slightly paler. Segment 10 dark brown, black apically; cerci black. Subgenital plate (Fig. 46) acutely pointed posteriorly, with long, dark setae around margin; laterotergites between subgenital plate and ninth tergum moderately sclerotized, posteriorly rounded, with evenly curved outer surface, often folded in dried specimens. Genital plates (Figs. 47, 48) widest near mid-length, with broad posterior lobes; axial portion not attaining posteromedial margin; apodemes short, less than half as long as plates.

Body length, male, about 10.7-11.6 mm. (holotype 11.3 mm.); female about 10.2-12.0 mm. (allotype 12.0 mm.). Fore wing, male, 10.5-11.8 mm. (holotype 10.5 mm.); female, 11.0-12.4 mm. (allotype 12.4 mm.).

Holotype male, collected 2 miles east of Walterboro, Colleton Co., South Carolina, 29 Oct. 1988, by Wes Bicha. Allotype, 2 miles east of Round O (name of village), Colleton Co., South Carolina, 29 Oct. 1988, Wes Bicha. Paratypes: SOUTH CAROLINA: Bamberg Co., S of Bamberg, 8 Oct. 1988 (2m, 2f); Calhoun Co., 5 mi. S of Sandy Run, 29 Oct. 1988 (1m); Colleton Co., 2 mi. E of Walterboro, 29 Oct. 1988 (4m, 3f), Round O, 29 Oct. 1988 (1m), 7 mi. S of Ruffin, 29 Oct. 1988 (1m, 1f); Edgefield Co., Big Hart Lake State Forest, 14 May 1988 (11m, 1f); Orangeburg Co., Holly Hill, 30 Oct. 1988 (3m); all collected by Wes Bicha; Kershaw Co., Camden, 26 Sept. 1930, T. H. Hubbell (1m, 1f). GEORGIA: Emanuel Co., 3 mi. W of Coleman Lake, 19 May 1989, WB (1m).

Holotype, allotype and 2 male paratypes in the SEM. Other paratypes are in the collection of Wes Bicha, the USNM, and the MCZ.

In structure of the genital bulb of males, *Panorpa hispida* somewhat resembles *P. palustris* Byers and *P. vernalis* Byers. It differs from both these species most conspicuously in wing pattern, having a complete pterostigmal band and the basal band only narrowly broken near its mid-length. The genital bulb is relatively much wider in *hispida* (width greater than height to apices of basistyles), and the ventral parameres have barbs along the mesal edge only (as in *vernalis* but differing from *palustris*). The thick apical setae of the basistyles are longer but fewer in number than those of *vernalis* and are divergent rather than subparallel (absent in *palustris*). The basistyles are much more deeply separated ventrally than in *palustris*; and the hypovalves are more widely divergent than in *vernalis*. Presence of laterotergites with smoothly curved outer surfaces (as contrasted with the convoluted, densely sclerotized laterotergites in females of many species) is diagnostic for females of *hispida*.

The name *hispida* (Latin, bristly) refers to the long, thick, black setae on the inner, ventral apex of the basistyle, as well as to the marginal setae of the hypovalves of the male, longer and darker than their counterparts in most species, and the setae on the subgenital plate of the female.

Panorpa scopulifera new species

Description based on 23 males, 8 females, pinned (12m, 3f of these originally preserved in alcohol).

Head: Dorsum, frons and most of rostrum dark yellowish brown; narrow dark brown zone around ocelli; apex of rostrum, including maxillary palps, usually brown. Scape, pedicel and basal half of first flagellomere sordid yellowish brown; flagellum dark brown to black, with 36 (holotype) to 40 flagellomeres, usually 36-37.

Thorax: Dorsum sordid dark yellowish brown without distinct markings; pleural surfaces, coxae and mera dull yellowish brown with scattered pale setae and a few dark setae on anterior surfaces of fore and middle coxae; legs yellowish brown with dark setae; tarsi slightly darker than legs except fifth tarsomeres dark gray.

Wings strongly tinged with pale yellowish brown, with brown markings. Apical band usually entire, with one or two small included pale spots in two autumnal males, two or more in all vernal individuals. Pterostigmal band complete but narrow near mid-length, not forked but apical branch represented by spot at posterior margin between M_3 and M_4. Marginal spot present, variable in extent, usually interrupted between R_{2+3} and R_{4+5} (holotype), thus two separate spots, that bordering R_{4+5} very small. Basal band usually broken behind M (holotype), otherwise extremely slender near mid-length. First basal and first humeral spots present.

Abdomen of male: All terga and sterna unevenly yellowish brown; tergal horn on sixth segment usually slender and slightly downcurved (holotype), more stout in a few males. Notal organ weakly developed, a broadly rounded median lobe bearing decurved black hairs, on tergum 3, and small peg on tergum 4. Genital bulb (Fig. 49) slightly wider than its length to ends of basistyles. Hypovalves slender, narrowing slightly toward tips, extending to ends of basistyles or somewhat shorter, divergent near base, with long hairs on mesal margins and scattered shorter hairs. Tergum 9 with two slender apical lobes slightly inclined toward each other, emargination between them roughly U-shaped. Cerci short, extending slightly from beneath ninth tergum. Basistyles with 1-4 thick, black, subparallel setae at ventromesal apex (2 on each basistyle in holotype, 2-3 in most males). Dististyles of roughly uniform thickness in basal two-thirds, then narrowing and curving to strongly sclerotized, acute apex. Inner basal cup shallow, with darkened rim produced to form short, blunt tooth on dorsomesal edge; about 12 short, sharply pointed, black setae along dorsal edge of cup near base of dististyle. Ventral parameres flattened, blade-like, abruptly narrowed shortly before acute apex, with barbs along inner edge only, increasing in length toward apex, longest ones extending only to ends of basistyles; free end of paramere not conspicuously curved, most darkly sclerotized along lateral margin. Dorsal parameres moderately sclerotized, palest toward apex, with thin-walled dorsal appendage directed toward base of aedeagus. Ventral valves pale, merging laterally with dorsal parameres; dorsal valves small, pale. No aedeagal hamulus, but sclerotized band connecting ventral parameres slightly thickened near mid-line.

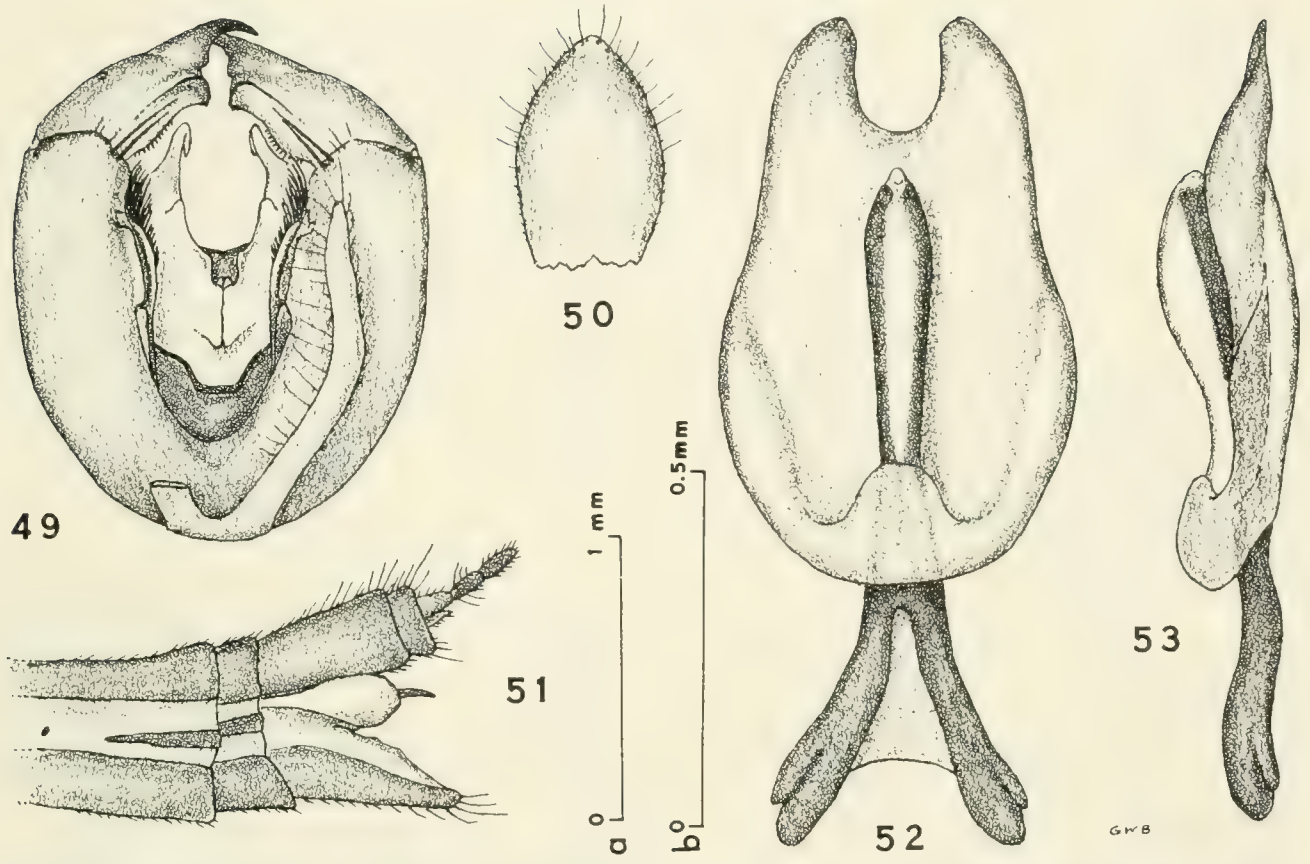
Abdomen of female: All terga and sterna unevenly sordid yellowish brown, darker in specimens pinned soon after capture (e.g., allotype). Cerci dark brown basally, terminal segment black. Subgenital plate (Fig. 50) rounded at apex. Prominent laterotergite at each side below ninth tergum, yellowish brown to pale brown, evenly rounded posteriorly (Fig. 51). Genital plates (Figs. 52, 53) with broad posterior lobes, median notch U-shaped; axial portion not extending to margin of notch; basal plate somewhat swollen (thickened) along lateral margins; apodemes only moderately divergent.

Body length, male, about 9 to 13 mm. (holotype 10.9 mm.); female, about 9 to 11 mm. (allotype 9.1 mm.). Length of fore wing, male, 10.1 to 12.5 mm. (holotype 11.5 mm.); female, 11.4 to 12.2 mm. (allotype 11.4 mm.). Individuals collected in spring are noticeably larger than autumnal ones.

Holotype male and allotype, 3 miles south-southwest of Mountsville, Laurens Co., South Carolina, 5 October 1977, George W. Byers (field cat., Laurens Co. no. 1). Paratypes: SOUTH CAROLINA: same data as holotype (4m, 3f); Laurens Co., Sumter National Forest, 9 mi. east of Clinton, 5 Oct. 1977, GWB (3m, 1f); Laurens Co., Laurens, 15 Sept. 1980, WB (2m); same but 27 May 1988, WB (3m, 3f); Abbeville Co., 15 Sept. 1980, WB (2m); Abbeville Co., Calhoun Falls, 29 May 1978, GWB (1 m); Anderson Co., 8 mi. N of Anderson, 1 Sept. 1991, WB (3m); Chester Co., 27 May 1984, WB (1m); Newberry Co., Whitmire, 6 and 27 May 1988, WB (2m); McCormick Co., Savannah River at U.S. Hwy. 378, 4 Oct. 1977, GWB (1m). GEORGIA: Franklin Co., 1 Sept. 1984, WB (1m); 2 mi. S of Carnesville, 15 Sept. 1991, WB (1m).

Holotype, allotype and 4 male, 3 female paratypes are in the SEM. Other paratypes are in collection of Wes Bicha, in the USNM, and the MCZ.

Panorpa scopulifera is very similar to *P. hispida* in most details of



Figs. 49-53. *Panorpa scopulifera*, n. sp. **49,** genital bulb, male holotype, ventral aspect; left hypovalve omitted. **50,** subgenital plate, female allotype, ventral aspect. **51,** terminal abdominal segments (8-11), allotype, left lateral aspect, to show laterotergite. **52,** genital plate, allotype, ventral aspect. **53,** same, right lateral aspect. Scale a, figs. 49-51; scale b, figs. 52-53.

structure and color, and the two are presumed to be closely related. The striking difference in males is that the ventral parameres are much shorter in *scopulifera*. (Latin *scopula* = a small brush or broom + ferre = to bear, referring to the short, brush-like ventral parameres.) Females of *scopulifera* may be recognized by their short, rounded laterotergites, which, however, resemble those of *P. pachymera*, n. sp., a regional species occurring farther to the west. In some dried specimens, the laterotergites may not be readily visible because of the upturned edges of the subgenital plate.

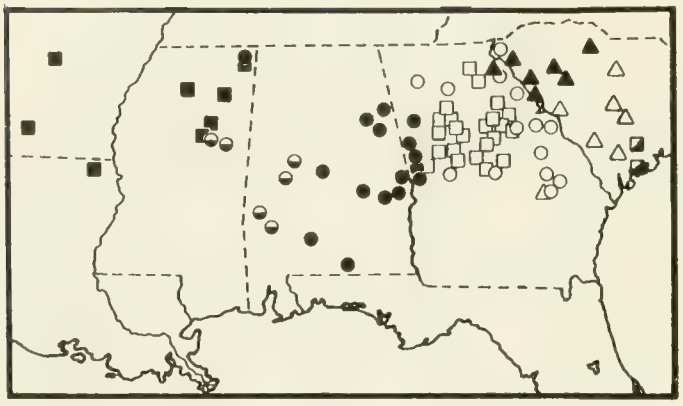
Available specimens of *P. scopulifera* and *P. hispida* indicate separate, rather limited ranges, *scopulifera* being a species of the piedmont and *hispida* occurring on the coastal plain (Map 5). Collecting to date has not yielded any specimens from the intervening area, but in the future these two forms may prove to be only subspecies of a single species.

At the type locality, *Panorpa scopulifera* was found on shaded clumps of honeysuckle in an undergrowth including also brambles, some woodbine (Virginia creeper) and young saplings of pine and red gum, in a wooded area composed almost wholly of pines. At another site in Laurens Co., South Carolina, and in McCormick Co., the habitat was nearly the same except that the woods included some more mature red gum trees and a few oaks and hickories, and the undergrowth included poison ivy, also trumpet vine (*Campsis radicans*) growing across the ground and up tree trunks. The occurrence of this and several other species of *Panorpa* in the Southeast on honeysuckle, poison ivy and associated broad-leaved plants possibly relates to (1) retention of moisture beneath such thickets, amid generally dry surroundings, (2) a concentration of other kinds of insects that, when dead, are the food of scorpionflies, and (3) presence of nearly horizontal leaf surfaces on which to stand.

Panorpa rufescens Rambur

This species has been reported from several southeastern states, including Florida, Georgia, North Carolina and Virginia (Carpenter, 1931) and Mississippi (Byers, 1962a), in addition to its northeastern range: New England states, New York, Pennsylvania, New Jersey and Maryland. Carpenter illustrated the male of *rufescens* (1931, fig. 20) as having very short, mesally curved ventral parameres with short apical barbs. This is the form found in the Northeast. Males from the southeastern states were found to have considerably longer ventral parameres, which, however, were shorter than those of nearly all other nearctic species and did not extend to the level of the outer ends of the basistyles. In wing maculation and other characters, these two forms were inseparable. Either of them would be identified as *rufescens* by existing keys. I have seen spring specimens of the northeastern form from as far south as eastern Virginia.

There is nothing in Rambur's description of *rufescens* that will differentiate it from several other species in which males have a horn-like process on the sixth abdominal segment. Accordingly,



Map 5. Geographical distribution of new species in the *Panorpa rufescens* group in southeastern United States. Solid circles - *P. ferruginea*; open circles - *P. pachymera*; half-shaded circles - *P. confinis*; open triangles - *P. hispida*; solid triangles - *P. scopulifera*; open squares - *P. acuminata*; half-shaded squares - *P. planicola*; solid squares - *P. rupeculana*. Each symbol represents one or more collections in a county.

it was necessary to refer to Rambur's type specimens, supposedly in the collection of Baron de Selys-Longchamps, in the Institut Royal des Sciences Naturelles de Belgique, Brussels. While three of the nine specimens of *rufescens* in the Selys collection are labelled "Coll. Latreille," none has any similar indication that it was formerly in the Rambur collection. One damaged male, however, is labelled "Am. Sept."; and Rambur said of *rufescens* "habite l'Amérique septentrionale." Following publication of his revision of the nearctic Mecoptera, in 1931, Carpenter had occasion to examine the specimens in the Selys collection. It was his opinion that none of the specimens in that collection was an original Rambur type (Carpenter, 1939) since none was labelled as a type. Years later, however, I found that one male (in a series of 3m, 5f and 1 without abdomen) did in fact bear a label, apparently attached by Esben-Petersen, ca. 1920, reading "Figure of appendices male, Type specimen," as well as others. Accepting Esben-Petersen's judgment, I designated this male as the lectotype of *rufescens* (Byers, 1962b).

Unfortunately, as it has turned out, the lectotype is a male of the southeastern form, that is, the form having somewhat longer ventral parameres with longer barbs on them. This selection was unfortunate because I now think that the northeastern form and the southeastern form are two different species. Carpenter must have noticed that the supposed type he examined was not the same, in detail, as what he had identified as *rufescens*. Having decided that it was not really the type, he wrote (Carpenter, 1939), "This opens again the question of the identity of *rufescens*, the type apparently being lost. It seems advisable, under the circumstances, to recognize *rufescens* as it has been treated in the past by Banks and myself."

At present, I agree with this view. The lectotype (i.e., the same individual that Esben-Petersen had labelled as "Type specimen" but that Carpenter rejected as an original type) does not appear to have been one of Rambur's specimens. It is, in fact, one of those labelled "Coll. Latreille." Although the "Neuroptera" from both Rambur's and Latreille's collections are now part of the Selys collection, I can find no indication that Rambur ever examined Latreille's specimens. And if the lectotype is not an original syntype, it has no status as a lectotype (Article 74a[v] of the International Code of Zoological Nomenclature).

Accordingly, the name *rufescens* needs to be associated with a neotype, since no original type is known to exist. And I agree with Carpenter that this should be a specimen of the northeastern form that was identified as *rufescens* by Banks and by Carpenter himself (cf. Figs. 63, 64). I have therefore selected as neotype a male that is pinned but otherwise intact in every respect and bears the following labels: "Laurel Lake, nr. Jacksonville, Vt., 10-VIII-1978, H. D. Pratt" and "*Panorpa rufescens* Rambur, Det. G. W. Byers 1985," in addition to a red label stating that this individual is the neotype. (Jacksonville is in Windham County, Vermont, about 6.4 km. north of the border with Massachusetts.) The specimen agrees in detail with the description and figures of *rufescens* in Carpenter's revision (1931: 236, fig. 20 - genital bulb of male, and fig. 83 - wing); it also agrees with the much more general description by Rambur. The neotype is in the SEM, to which it was generously contributed by Dr. Harry D. Pratt several years ago.

That being done, the southeastern form is left without a name. Following is its taxonomic description:

Panorpa ferruginea new species

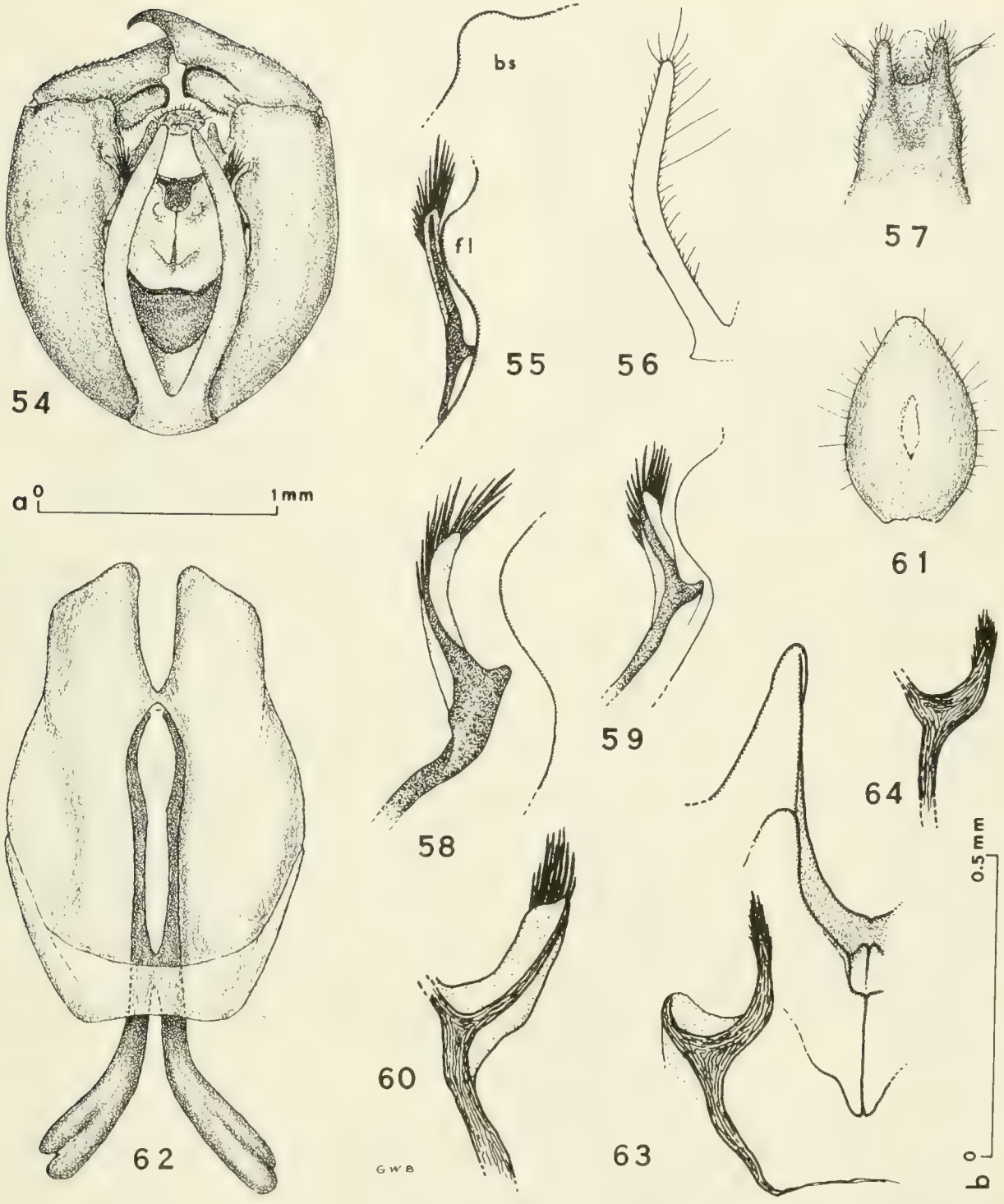
Description based on 51 males, 27 females, pinned.

Head: Dorsum, frons and rostrum (including palps) dark amber brown; dark ring around each ocellus. Scape, pedicel and most of basal flagellomere dark yellowish brown; flagellum black, with 37-41 flagellomeres (average 38).

Thorax: Dorsum unevenly dark yellowish brown, without distinct markings; pleural surfaces, coxae and mera dark yellowish brown with fine, silvery pubescence on mesothorax and metathorax and scattered yellowish hairs, longest and most dense on anterior surfaces of coxae; a few black setae on anterior surface of middle coxae and, in several individuals, across anterior, apical edges of hind coxae. Legs and tarsi dark yellowish brown, except fifth tarsomeres somewhat blackened.

Wings strongly tinged with yellowish brown, with dark brown bands and spots. Apical band entire, rarely with a small included pale spot. Pterostigmal band complete, often narrowed just behind M_{1+2}, unbranched but outer branch represented by spot at wing margin between M_3 and M_4. Marginal spot slender, extending from C to slightly behind R_{4+5} or interrupted near R_{2+3} to form two spots. Basal band usually interrupted near M to Cu_1, unbroken but narrowly constricted near M in a few individuals. Anterior basal spot present, approximately R to Cu_2; faint indication of posterior basal spot near end of A_2. First humeral spot present, slightly beyond h.

Abdomen of male: Terga 2-5 unevenly yellowish brown, corresponding sterna pale yellowish brown; tergal horn on segment 6 longer than width at base (lateral aspect), tip slightly downcurved; notal organ weakly developed, with sparse, decurved, black hairs on middle posterior margin of tergum 3 and (usually concealed) sclerotized peg on tergum 4. Genital bulb (Fig. 54) broad, slightly wider across apices of basistyles than length of bulb excluding dististyles. Hypovalves slender, widest near mid-length, then tapering toward narrowly rounded apex, extending almost to tips of basistyles; some hairs on mesal margins 2-3 times as long as width of hypovalve (Fig. 56). Tergum 9 (Fig. 57) with U-shaped emargination; apical setae on posterolateral lobes black, strongly curved mesad. Inner, apical margin of basistyle a broadly rounded lobe with a few hairs but without thick, black setae (holotype), or rarely with one or two such setae. Basistylar flange thin, rounded. Dististyles thick in basal two-thirds, narrowing and curving evenly to acute, densely sclerotized apex. Inner basal cup of dististyle shallow, its margin darkly sclerotized except near base, with low, angular, dorso-mesal tooth and row of 9-14 short, thick, sharply pointed setae along dorsal margin. Ventral parameres (Fig. 55) short, their terminal barbs not reaching or barely reaching apex of basistyles; free portion (beyond lateral branch) acutely tipped,



Figs. 54-62. *Panorpa ferruginea*, n. sp. **54,** genital bulb, male holotype, ventral aspect (most hairs omitted). **55,** right ventral paramere, holotype, shown in relation to basistylar flange (fl) and ventro-mesal apex of basistyle (bs). **56,** left hypovalve, holotype, showing relative lengths of marginal setae. **57,** ninth abdominal tergum, tergum 10 (partially concealed), tergum 11 (indicated by dashed line) and cerci, paratype from Heard Co., Georgia. **58,** right ventral paramere, paratype from Covington Co., Alabama, shown in relation to basistylar flange. **59,** same, paratype from Lee Co., Alabama. **60,** left ventral paramere, paratype from Heard Co., Georgia (most atypical form assigned to this species). **61,** subgenital plate, female allotype, ventral aspect. **62,** genital plate, allotype, ventral aspect. **Figs. 63-64.** *Panorpa rufescens* Rambur. **63,** left ventral paramere, shown in relation to dorsal paramere, ventral and dorsal valves of aedeagus, male from Framingham, Massachusetts. **64,** left ventral paramere, male from Williamsburg, Virginia. Scale a, figs. 54, 56-57, 61; scale b, figs. 55, 58-60, 62-64.

bowed ventrad, with few (4-8) barbs on outer surface shortly before tip but greater number along inner and dorsal surfaces and directed primarily dorsad (thus sometimes not easily seen in ventral, or posterior, aspect); terminal barbs often appressed to basistyle in dried specimens. Dorsal parameres dark brown mesally near base, paler toward apex yet firmly sclerotized, with lightly sclerotized dorsal appendage bent back toward base of aedeagus. Ventral valves only slightly sclerotized, together forming a V-shaped structure usually projecting from ventral surface of aedeagus (holotype), less often barely projecting. Aedeagal hamulus absent, but sclerotized band between ventral parameres slightly widened near mid-line. Segments 10 and 11 (telescoped into 10) usually clearly visible between bases of dististyles; cerci short.

Abdomen of female: Terga and sterna unevenly sordid dark yellowish brown; cerci black. Subgenital plate nearly flat, with upturned edges, its pointed or narrowly rounded apex bent downward in some dried specimens; longer marginal setae about one-fourth to one-third of greatest width of plate; an elliptical, weakly sclerotized, nearly transparent area (Fig. 61) on mid-line near mid-length of plate (between opaque structures on dorsal surface of plate). No laterotergites. Genital plates (Fig. 62) generally as in *P. rufescens*, widest near mid-length, with apical (posterior) projections of distal plate broad, their posterior margins slanting cephalad and laterad from apices; long-oval swelling at each side, on ventral surface of basal plate; axial portion almost reaching posterior margin of apical plate in narrow median notch; apodemes widely divergent laterad.

Body length, male, approximately 10 to 12 mm. (holotype 11.6 mm.); female, about 7.7 to 11 mm. (allotype 10.4 mm). Length of fore wing, male, 9.4-11.7 mm. (holotype 10.9 mm.); female, 8.7-11.8 mm. (allotype 10.1 mm.).

Holotype male, 1 mi. N of Fairfax, Chambers Co., Alabama, 1 October 1977, George W. Byers (field cat. no. 1). Allotype and 5m, 4f paratypes, same data as holotype. Additional paratypes: ALABAMA: Bibb Co., Woodstock 5 Sept. 1987, WB (1m); Calhoun Co., E of Piedmont, 13 Sept. 1980, WB (1m); Chambers Co., Fairfax, 24 Sept. 1988, WB (2m); Cherokee Co., 1 mi. SW of Gaylesville, 1 Oct. 1988, WB (1m, 2f); Covington Co., Wing (Conecuh National Forest), 24 Oct. 1985, WB (2m); Elmore Co., 6 mi W of Wetumpka, hwy. 14, 29 Sept. 1977, GWB (3m, 3f); Etowah Co., 29 May 1989, WB (1m); Lee Co., Wilmore Lake, 3 mi. SE of Auburn, 30 Sept. 1977, GWB (1m, 1f), Auburn, SW edge of Auburn Univ. campus, 30 Sept. 1977, GWB (6f); Macon Co., Tuskegee, 20 Oct. 1984, WB (1m), 5 Sept. 1987, WB (2m), 6 Sept. 1987, WB (2m); Monroe Co., Little River State Park, 24 May 1986, WB (1m). GEORGIA: Carroll Co., Tanner State Park, 30 Aug. 1984, WB (1f); Harris Co., W of Pine Mountain, 25 Sept. 1988, WB (1m); Heard Co., Glovers Creek, 30 Aug. 1984, WB (5m); Heard Co., 18 Sept. 1988, WB (3m), 24 Sept. 1988, WB (9m, 1f); Paulding Co., W of Dallas, 30 Aug. 1984, WB (2m), 30 Sept. 1984, WB (1m); Troup Co., 2 mi. NE of West Point, 1 Oct. 1977, GWB (7m, 8f). MISSISSIPPI: Alcorn Co., 11 mi. SE of Corinth, 7 June 1958, GWB (2m, 3f).

Holotype, allotype and 30 paratypes are in the SEM; other paratypes in WB collection and in the USNM, UMMZ and MCZ.

Of all the "*rufescens*-like" scorpion-flies in the southeastern states, *P. ferruginea* has the closest resemblance to *rufescens* because of the short, slender ventral parameres in the male, in addition to more obvious characters such as wing maculation and shapes of dististyles and hypovalves (Figs. 63, 64). The genital plates of females also rather closely resemble those of *rufescens*. Either sex would be identified as *rufescens* by existing keys.

The most closely related species, however, appears to be *Panorpa confinis* n. sp., which like *ferruginea* has short ventral parameres. Unlike *ferruginea*, *P. confinis* has two or three conspicuous thick, black setae on the inner, ventral apex of each basistyle, and the ventral parameres are so short and so close against the basistyles that they are often concealed from view by the hypovalves.

In males judged to belong to *P. ferruginea*, there is some variation in the ventral parameres, as shown in figures 55, 58-60. Part of such variation is probably a result of uneven shrinkage of the membranous parts and consequent bending and twisting of these parameres. But there is also noticeable variation in the number of barbs. In some males, the basal parts of the ventral valves of the aedeagus protrude somewhat ventrad, while in others they remain approximately at the level of surrounding membranous areas. This difference also appears to be a post-mortem result of preservation.

The habitat at the type locality fairly represents the kinds of places where *P. ferruginea* has been found. It was a pine woods with a scattering of red gum, hickory and oak trees, with dogwood as a common understory tree. Much of the ground was covered with fallen dried pine needles. The Panorpas (both *ferruginea* and *neglecta*) were taken from dense growths of honeysuckle, brambles and greenbriars, mainly in areas that on sunny days would be shaded (the sky was completely overcast at the time of collection, yet bright).

Panorpa confinis new species

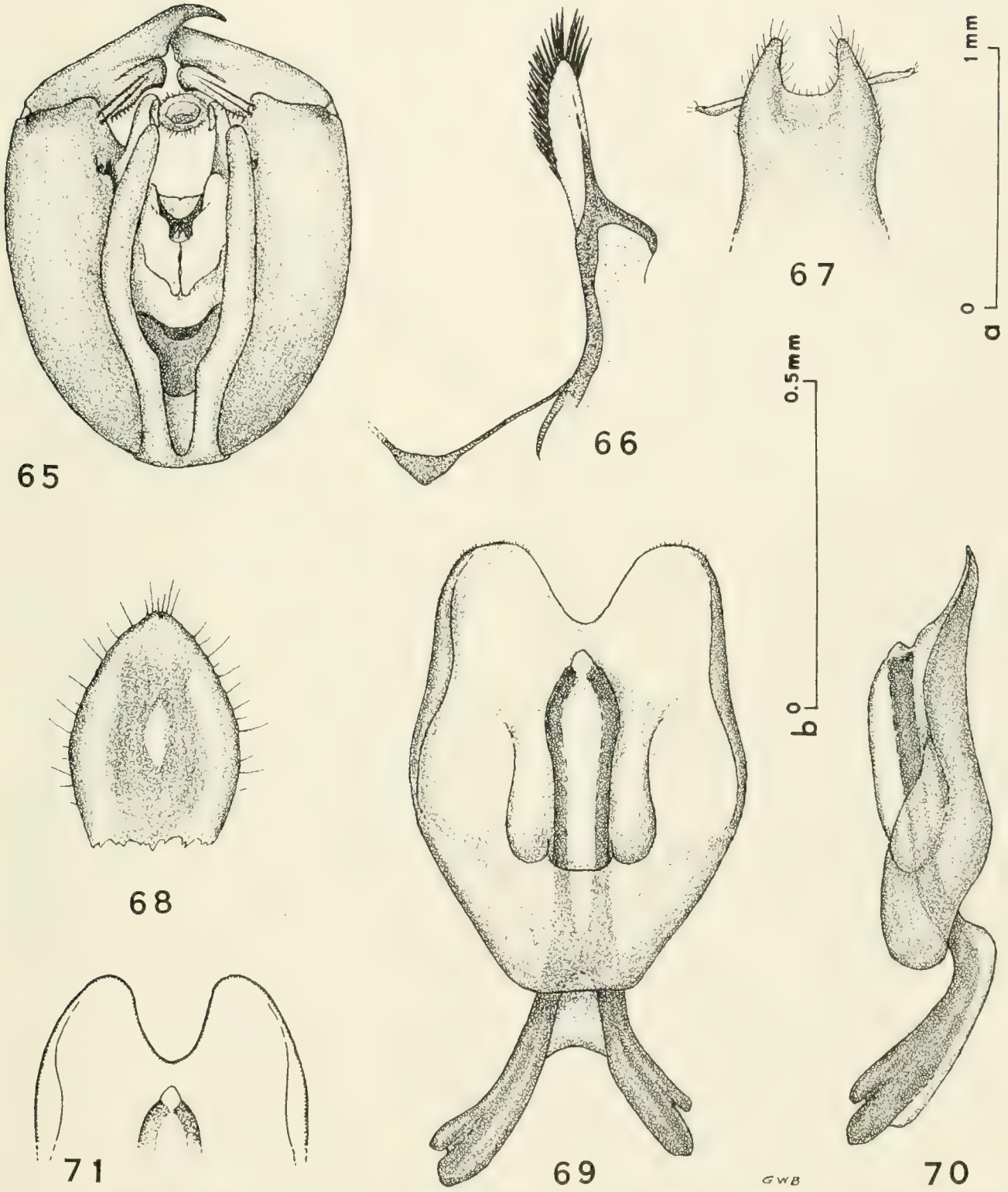
Description based on 12 males, 11 females, pinned (4 of the males initially preserved in alcohol), 10 males, 5 females in alcohol.

Head: Dorsum, frons and rostrum dark yellowish brown (holotype) to unevenly dark amber brown except black crescent above each ocellus; maxillary and labial palps amber brown, apical half of each terminal segment dark brown to black. Scape amber brown, pedicel and first flagellomere a little darker, blackened apically in some specimens; flagellum black, with 36-39 flagellomeres (holotype 38).

Thorax: Dorsum unevenly sordid dark yellowish brown, without any pattern of markings; pleural surfaces, coxae and mera dark yellowish brown in specimens pinned soon after capture, much paler in those preserved in alcohol; fine whitish pubescence on sides of mesothorax and metathorax; scattered golden-yellow hairs longest and most dense on anterior surfaces of coxae; a few dark hairs among yellow ones near apex of middle coxae. Legs yellowish brown, tarsi only slightly darker, with chiefly yellowish hairs.

Wings tinged with pale yellowish brown to light grayish brown, bands and spots brown to dark brown. Apical band with included pale areas variable in number and extent and concentrated near apical margin of wing; band fragmented in some specimens (including holotype), especially those collected in spring, complete in some autumnal ones. Pterostigmal band complete but usually very narrow at M_{1+2}, unbranched but outer branch represented by small spot between M_3 and M_4 near wing margin. Marginal spot small, usually between C and R_{2+3}; small spot also behind R_{4+5}, enclosing nygma. Basal band narrowly to widely interrupted near mid-length, generally between M and Cu_1, thus represented by two spots. Anterior basal spot and first humeral spot both present but latter very small in most specimens.

Abdomen of male: Terga 2-5 unevenly yellowish brown, corresponding sterna slightly paler; segments 6-9 amber brown; tergal horn on segment 6. Notal organ weakly developed, with numerous stiff, decurved black hairs on ventral and posterior surfaces of broad, slightly protruding median lobe on tergum 3 and short, sclerotized peg on anterior tergum 4. Genital bulb (Fig. 65) slightly longer than wide (dististyles excluded). Hypovalves deeply separated, narrowest in basal one-third, tapering slightly toward apex; about 15-20 long, thin, blackened setae along inner margin and on apex of each hypovalve, most a little more than twice width of hypovalve. Tergum 9 (Fig. 67) with posterior lobes roughly triangular, twice as wide at base as at mid-length; marginal setae fairly evenly distributed. Inner subapical surface of each basistyle with 2-4 (usually 2, as in holotype) thick, black setae extending into basal cups of dististyles. Flange on basistyle widest apically,



Figs. 65-71. *Panorpa conjunis*, n. sp. **65,** genital bulb, male holotype, ventral aspect (most hairs omitted). **66,** right ventral paramere, topotypic male paratype, ventral aspect. **67,** ninth abdominal tergum, male paratype. **68,** subgenital plate, female allotype, ventral aspect. **69,** genital plate, allotype, ventral aspect. **70,** same, right lateral aspect. **71,** distal (apical) plate, female from Choctaw Co., Mississippi, showing narrower, less bluntly rounded posterior lobes. Scale a, figs. 65, 67-68; scale b, figs. 66, 69-71.

tapering basad. Outer surface of dististyles nearly straight to slightly concave before mid-length; apical one-third darkened, evenly curved toward tip. Inner basal cup of dististyle shallow, with darkly sclerotized margin except toward base, with low dorso-mesal tooth (or angle) and 6-9 sharply tipped, short, black setae along dorsal margin near base. Ventral parameres (Fig. 66), short, with darkly sclerotized ventral band in free portion not reaching tip; paramere somewhat spatulate in fluid-preserved males but variously distorted in dried specimens; position usually near inner wall of basistyle, with terminal barbs not extending far beyond flange; 4-6 barbs on outer subapical edge, larger number along inner (or dorsal) edge. Dorsal parameres moderately sclerotized basally, yellowish toward apex, with flat, lightly sclerotized apical appendage bent back toward base of aedeagus. Ventral valves pale, near-white to slightly yellowish. Aedeagal hamulus absent, but sclerotized band connnecting ventral parameres noticeably widened medially (Fig. 66). Segments 10 and 11 usually visible between bases of dististyles; cerci prominent.

Abdomen of female: Terga and sterna unevenly dark yellowish brown to brown; cerci brown near base, mostly black. Subgenital plate (Fig. 68) broad at base, subacute at apex, with elliptical translucent area near middle (between more opaque structures on dorsal surface); long marginal setae sparse. Laterotergites small, concealed in pinned specimens, not easily visible in fluid-preserved females, connected broadly to sclerotized folds partially enclosing genital plates. Apical genital plate (Fig. 69) with broadly rounded (allotype) to more narrowly rounded (Fig. 71) or bluntly pointed posterior lobes; axial portion abruptly curved above basal plate in lateral aspect, apical end not reaching margin of U-shaped or broadly V-shaped median notch; longitudinal swelling at either side of axial portion (ventral aspect), in addition to marginal swelling of basal plate; apodemes widely divergent, with lightly sclerotized dorsal ridge on each (Fig. 70), making apodemes appear unusually thick.

Body length, male, about 9 to 13 mm. (holotype 11.2 mm.); female, about 9.5 to 12 mm. (allotype 9.1 mm.). Length of front wing, male, 9.3 to 11.6 mm. (holotype 11.0 mm.); female, 10.3 to 12.0 mm. (allotype 11.2 mm.). In general, autumnal individuals slightly smaller than spring ones.

Holotype male, Payne Lake, 24 mi. SE of Tuscaloosa, Hale Co., Alabama, 25 May 1978, G. W. Byers and C. W. Young (GWB field cat., Hale Co. no. 1). Allotype female, Talladega National Forest, 3 mi. E of Duncanville, Tuscaloosa Co., Alabama, 29 Sept. 1977, G. W. Byers. Additional paratypes: ALABAMA: Hale Co., same data as holotype (14m, 6f); Tuscaloosa Co., same data as allotype (3m, 2f); Choctaw Co., 0.3 mi. E of Butler, 11 April 1982, WB (2m); Clarke Co., Coffeeville, 11 April 1982, WB (2m). MISSISSIPPI: Choctaw Co., Ackerman, 24 Sept. 1977, GWB (3f); Oktibbeha Co., State College, 16 Nov. 1981, W. H. Cross (1f), 20 April 1950, R. Humphrey (1f), 10 April 1961, J. Boyd (1f), 24 June 1961, M. J. Wade (1f).

Holotype, allotype and most paratypes are in the SEM. Four paratypes in collection of Wes Bicha, one in Mississippi State University.

Panorpa confinis has both an autumnal and a vernal flight period, that is, two generations a year. The holotype was selected from the late May collection because of its better condition.

This species seems to bear much the same sort of relationship to *P. ferruginea* as *P. insolens* Carpenter does to *P. helena* Byers. That is, the most conspicuous difference is that males of *confinis* have thick, black setae on the inner, apical surface of the basistyle, whereas those of *ferruginea* do not. There are apparently also minor but consistent differences in the shapes of the ventral parameres and the basistylar flanges. The ventral parameres somewhat resemble those of *P. vernalis*, which is known from southwestern Mississippi, but are shorter in *confinis* and have the sclerotized band abbreviated. Also the wing markings are very different in these two species. In females, the swellings alongside the axial portion of the genital plates, the rounded lobes on the apical plate (as contrasted with diagonally truncate in *ferruginea*), and the abrupt bend in the axial portion above the basal plate are diagnostic for *confinis*.

Panorpa confinis takes its name (Latin *confinis* = adjoining, lying adjacent, or neighboring) from the fact that its range as now known is contiguous with that of *ferruginea*. Not only is *ferruginea* geographically its nearest neighbor but also apparently its nearest kin, to judge from similarity of structure and color. Future biological investigations may show that *confinis* and *ferruginea* are only geographical races of a single species.

Panorpa pachymera new species

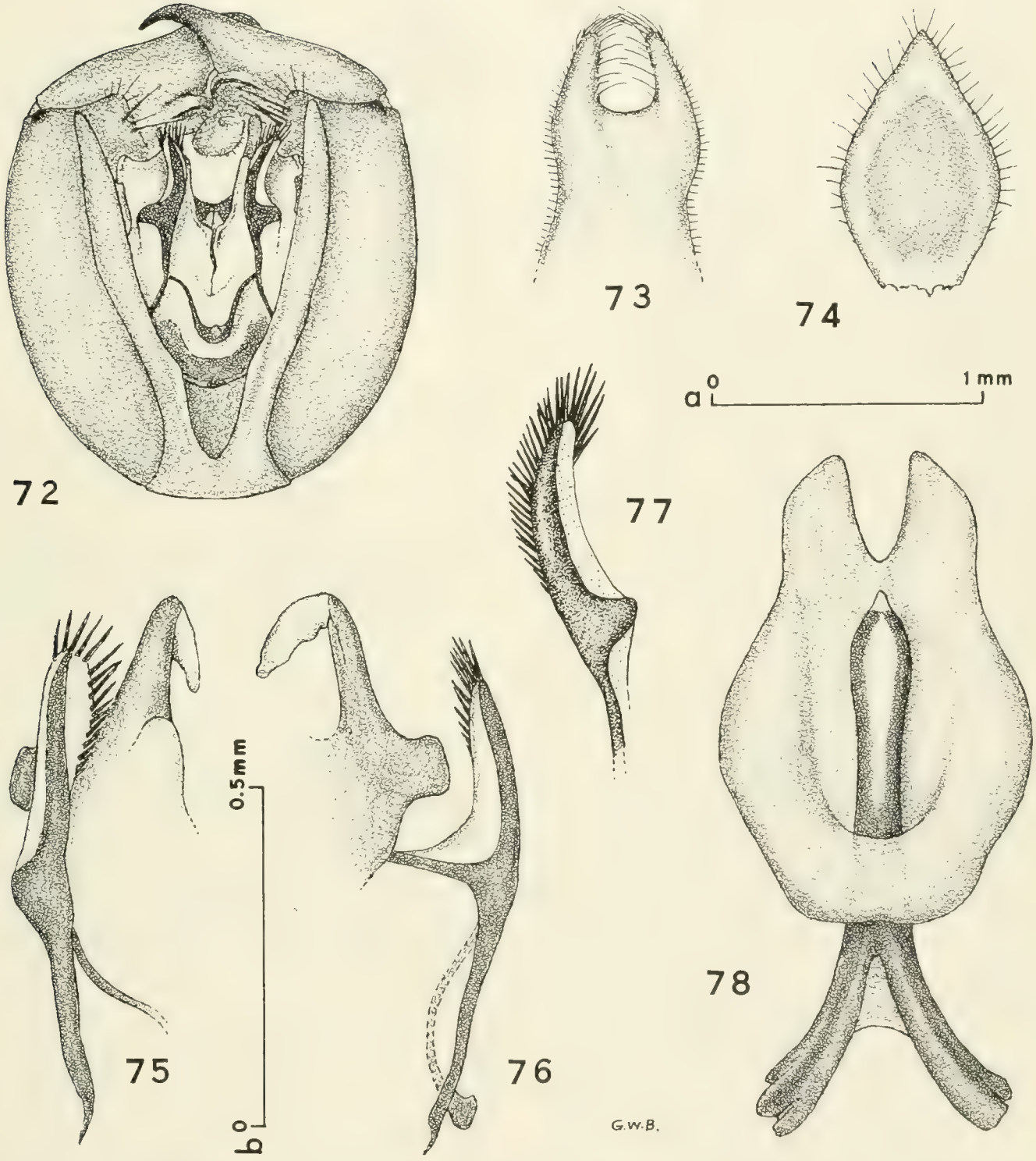
Description based on 66 males, 12 females, pinned but most initially preserved in alcohol.

Head: Uniformly amber brown except for blackened crescent above each ocellus and yellowish brown on sides of rostrum near apex. Maxillary and labial palps yellowish brown with darkened tips. Scape and pedicel dark yellowish brown, flagellum black except base of first flagellomere brown; 37-38 flagellomeres (holotype 38, right antenna broken at 25th flagellomere).

Thorax: Dorsum unevenly sordid grayish brown, without any distinct markings; pleural surfaces, coxae and mera yellowish brown with fine whitish pubescence on mesothorax and metathorax and scattered dark yellowish hairs longest and most dense on anterior surfaces of coxae; sparse black setae on anterior, subapical surfaces of middle coxae and along apical edges of hind coxae. Legs and tarsi yellowish brown, especially tarsi appearing darker because of abundant, small black setae.

Wings moderately to strongly tinged with yellowish brown, bands and spots dark brown. Apical band entire or with enclosed pale areas variable in number and size. Pterostigmal band complete, often narrowed behind M_{1+2}, unbranched but outer branch represented by spot of variable extent at margin between M_3 and M_4. Marginal spot small, usually extending from C to R_{2+3} and sometimes a smaller spot behind R_{4+5}. Basal band usually interrupted behind M (as in holotype), less often (in 10 of 54 specimens) complete. Anterior basal spot present, usually extending from R to Cu_2. First humeral spot present, ordinarily between C and R, slightly beyond h.

Abdomen of male: Terga 2-5 yellowish brown, corresponding sterna slightly paler, segments 6-9 amber brown; tergal horn on segment 6 short, thick, slightly downcurved, with apical brush of golden hairs on underside. Notal organ only weakly developed, with stiff, decurved black hairs on broad, scarcely protruding median lobe on tergum 3 and a sclerotized peg (ordinarily concealed) on tergum 4. Genital bulb (Fig. 72) broad, slightly wider at greatest width than its length excluding dististyles (the position of which varies). Hypovalves deeply separated, widest near mid-length, tapering gradually toward base and apex; about 10 long, thin, blackened setae along inner margin and on apex of each hypovalve, some twice width of hypovalve. Tergum 9 (Fig. 73) with brush of dark, inwardly curved setae at apex of each posterior lobe, several long, dark setae along mesal margins of lobes; numerous short, nearly erect setae on sides of tergum. Inner, subapical surface of basistyle with 0-4 thick, black setae, often varying in number from one basistyle to the other in an individual. Basistylar flange nearly truncate to broadly and slightly rounded, tilted dorsad at distal end. Outer surface of dististyles slightly convex between base and mid-length; outer one-third curved evenly to densely sclerotized apex. Inner basal cup of dististyle shallow, with darkly sclerotized margin except toward base, with low dorso-mesal tooth and 6-8 short, thick, sharply tipped black setae on dorsal margin near base. Ventral parameres (Figs. 75-79) short, thick, generally about half distance from inner edge of basistyle to mid-line (i.e., closer together than in similar species such as *ferruginea* and *confinis*), extending to end of basistyle, with terminal barbs in some individuals pressed against basal cup of dististyle; free portion longitudinally about half scle-



Figs. 72-78. *Panorpa pachymera*, n. sp. **72,** genital bulb, male holotype, ventral aspect (most hairs omitted). **73,** ninth abdominal tergum, topotypic male paratype. **74,** subgenital plate, female allotype, ventral aspect. **75,** left ventral and dorsal parameres, topotypic male paratype, ventro-mesal aspect to show barbs primarily along dorsal edge of ventral paramere. **76,** same individual, left lateral aspect. **77,** right ventral paramere, ventral aspect, male paratype from Warren Co., Georgia. **78,** genital plate, allotype, ventral aspect. Scale a, figs. 72-74; scale b, figs. 75-78.

rotized, half membranous, strongly bowed ventrad, with 5-7 barbs on outer subapical surface, greater number along inner, dorsal surface, often mostly concealed in ventral aspect. Dorsal parameres brown mesally near base, moderately sclerotized, yellowish brown toward apex, with slightly sclerotized apical appendage bent back toward base of aedeagus. Ventral valves pale, lightly sclerotized. Aedeagal hamulus absent, but broadly V-shaped sclerotized band between ventral parameres somewhat widened near mid-line. Segments 10 and 11 (inserted into 10) and sometimes posterior lobes of ninth tergum visible between bases of dististyles; cerci short.

Abdomen of female. Terga and sterna sordid dark yellowish brown; cerci dark brown to black except membranous areas pale. Subgenital plate broad at base, acutely tipped, with upturned edges a little paler than most of plate (Fig. 74); major marginal and terminal setae long, black, about one-fourth to one-third of greatest width of plate, about 10 in number on each side, 4 on underside just before apex; 7-8 black setae at each side on dorsal surface of plate, near edge, directed mesad (subgenital plate of allotype mounted with dorsal side up to show these setae, which are peculiar to this species). Laterotergites small, concealed in pinned specimens by upturned edges of subgenital plate. Genital plates (Fig. 78) widest near mid-length, with broad posterior lobes on apical plate, their outer margins slanting cephalad and laterad; axial portion not reaching posterior margin in narrow median notch; apodemes moderately divergent.

Body length, male, about 9 to 10 mm. (holotype and most males near 10 mm.); female, about 8 to 10 mm. (allotype 9 mm.). Length of fore wing, male, 8.9 to 12.3 mm. (holotype 11.6 mm.); female, 11.5 to 12.6 mm. (allotype 12.0 mm.).

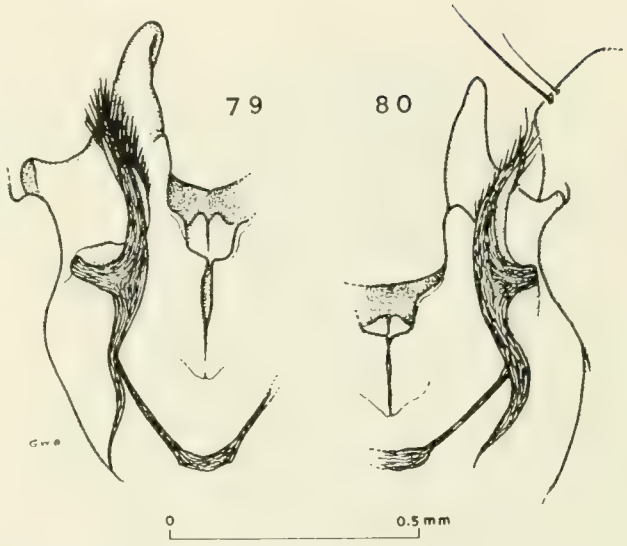
Holotype male, 3 mi. N of Camak, Warren Co., Georgia, 18 May 1989, Wes Bicha. Allotype and 10 male, 1 female paratypes, same data as holotype. Additional paratypes: GEORGIA: Baldwin Co., 1 mi. E of Milledgeville, 15 Sept. 1990, WB (1m); Cherokee Co., 31 Aug. 1991, WB (4m, 1f); Elbert Co., Rose Hill, 8 mi. E of Elberton, 29 May 1978, GWB (2m, 1f); Emanuel Co., 3 mi. W of Coleman's Lake, 19 May 1989, WB (2m); Franklin Co., 1 Sept. 1984, WB (4m); same but 15 Sept. 1991, WB (1m); Gordon Co., 20 May 1986, WB (3m, 2f); Hancock Co., 3 mi. E of Sparta, 15 Sept. 1990, WB (3m); Jefferson Co., 3 mi. W of Wrens, 17 May 1989, WB (1m, 3f); Jenkins Co., 8 mi. W of Millens, 19 May 1989, WB (5m); McDuffie Co., 16 May 1989, WB (2m); Monroe Co., 27 Sept. 1992, WB (1m); Richmond Co., North Augusta, 10-11 May 1989, WB (18m, 3 f); Taliaferro Co., 2 mi. S of Lyneville, 15 Sept. 1990, WB (1m); Upson Co., 27 Sept. 1992, WB (5m). SOUTH CAROLINA: Oconee Co., 1 Sept. 1984, WB (3m).

Holotype, allotype and four paratypes are in the SEM. Other paratypes have been returned to the collector, Wes Bicha.

Most available specimens of *Panorpa pachymera* were collected in spring, but the species also has an autumnal period of emergence, therefore is included here. It is not conspicuously different from *P. ferruginea* of western Georgia and Alabama. The ventral parameres in the male are both longer and thicker than those of *ferruginea* and are set much nearer the mid-line of the aedeagus (as contrasted with close to the inner surface of the basistyle in *ferruginea*), often concealing the dorsal parameres. Also the flange on the basistyle is less prominent than that in *ferruginea* and is more broadly rounded if not plainly truncate. Thick, black setae are present on the inner, ventral apex of the basistyle (but in variable numbers) in *pachymera*, while these are absent in *ferruginea*. The black, inwardly directed setae on the dorsal edges of the subgenital plate appear to be diagnostic for females of *P. pachymera*.

Wes Bicha has collected spring specimens in northern Florida (Santa Rosa Co.) that possibly belong to this species. Because of perceptible differences in male genital structures (compare Figs. 79 and 80) these are not made paratypes of *pachymera*.

The name *pachymera* is derived from Greek (*pachys*, thick + *meros*, a part), referring to the longer, thicker ventral parameres in this species as compared to those of the similar *P. ferruginea*.



Figs. 79-80. *Panorpa pachymera*, n. sp. **79,** left ventral and dorsal parameres and ventral and dorsal aedeagal valves, male paratype from Richmond Co., Georgia. **80,** right ventral paramere and associated structures, male from Santa Rosa Co., Florida, assigned to *pachymera* with some doubt (not a paratype). Scale, both figures.

The occurrence of *Panorpa pachymera* at the type locality (3 miles north of Camak, Warren Co., Georgia) is described by Wes Bicha (in a letter) as "in the most typical southern habitat: on poison ivy and honeysuckle at the edge of a mixed woods." At this site, the woods was chiefly red gum with occasional pines, but with no stream nearby. The open area bordering the woods appeared to be cleared as a right-of-way for an electric power line.

Panorpa acuminata new species

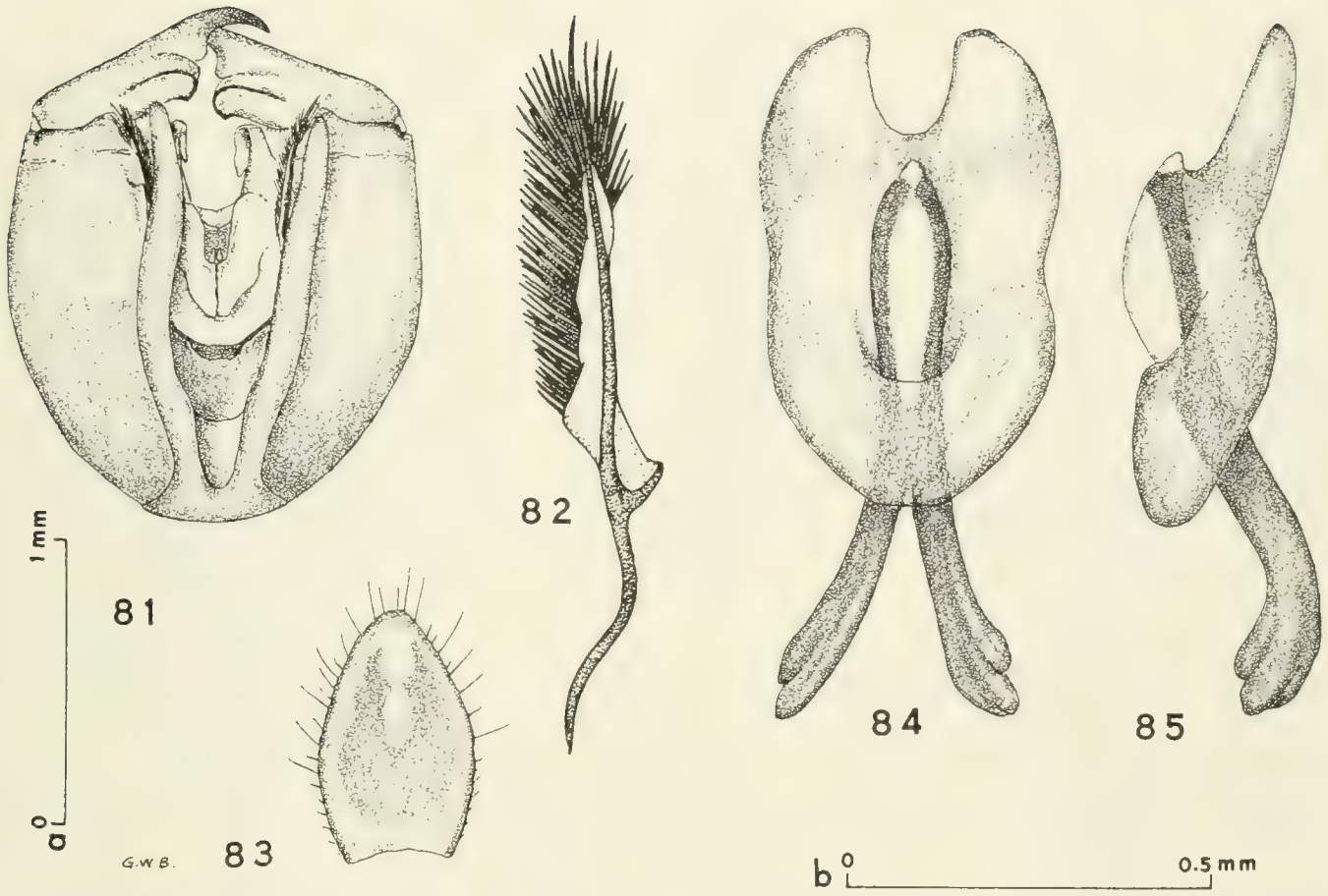
Description based on 39 males, 12 females, pinned.

Head: Dorsum and rostrum unevenly amber brown except for blackened crescent above each ocellus. Palps only slightly darkened apically. Scape, pedicel and approximately basal half of first flagellomere dark yellowish brown; flagellum black, with 38 to 40 flagellomeres (38 in holotype, 40 in allotype, but same variation in both sexes).

Thorax: Dorsum unevenly dark yellowish brown, without markings; pleural surfaces, coxae and mera sordid dark yellowish brown with fine whitish or silvery pubescence on mesothorax and metathorax (visible only at certain angles of illumination) and scattered dark yellowish hairs longest on anterior surfaces of coxae; sparse black hairs among yellow ones on middle coxae. Legs and tarsi yellowish brown with golden-yellow hairs; apical tarsomeres brownish.

Wings tinged with yellowish brown; bands and spots dark brown. Apical band usually entire but with small included pale spot in a few autumnal individuals, two or three small pale spots in those collected in May. Pterostigmal band complete but narrowed behind M_{1+2} (interrupted from M_1 to near M_4 in one female), not forked but distal branch represented by small spot at margin between M_3 and M_4. Marginal spot small, extending from C to R_{2+3}, with a small spot just behind R_{4+5} in a few individuals. Basal band usually broken near mid-length, behind M, but complete by a slender connection in four paratypes. Anterior basal spot and first humeral spot present, latter variable in extent, usually from C to R, slightly beyond h.

Abdomen of male: Terga 2-5 dull yellowish brown (holotype) to sordid dark yellowish brown, corresponding sterna slightly paler,



Figs. 81-85. *Panorpa acuminata*, n. sp. **81,** genital bulb, male holotype, ventral aspect (hairs omitted). **82,** right ventral paramere, ventral aspect, male paratype from Oglethorpe Co., Georgia. **83,** subgenital plate, female allotype, ventral aspect. **84,** genital plate, allotype, ventral aspect. **85,** same, right lateral aspect. Scale a, figs. 81, 83; scale b, figs. 82, 84-85.

segments 6-9 unevenly amber brown; tergal horn on segment 6 slightly downcurved apically. Notal organ weakly developed, with sparse stiff, decurved black hairs on broad, scarcely protruding lobe on tergum 3 and a short, thick median peg (almost knob-like in holotype) on anterior tergum 4. Genital bulb (Fig. 81) about as wide at widest point as its length, excluding dististyles. Hypovalves widest near mid-length, tapering gradually toward base and apex; longer setae along mesal margin and at apex about 12 in number and about twice as long as width of hypovalve. Tergum 9 with posterior lobes parallel, of approximately uniform width throughout, space between them nearly rectangular; apical hairs on lobes yellowish brown, inclined somewhat mesad. Inner, subapical margin of basistyle with 0-2 thick, black setae, usually none (as in holotype) and number sometimes varying from one basistyle to the other in one individual; combinations of setae 0-0 (11 males), 0-1 (2m), 1-1 (4m), 1-2 (4m) and 2-2 (5m). Basistylar flange rounded at apical end, tapering basally. Outer surface of dististyles straight to slightly concave in basal two-thirds, then evenly curved to apex. Inner basal cup of dististyle shallow, inner surface nearly flat to slightly concave, with darkly sclerotized margin except toward base; margin forming blunt dorso-mesal tooth, or angle; 6-9 short, thick, sharply tipped black setae on dorsal margin of cup near base of dististyle. Ventral parameres (Fig. 82) long, slender, with acuminate tips extending to or beyond ends of terminal barbs, curved slightly laterad near apex in several males, including holotype; small group of 6-8 barbs on outer, subapical surface of paramere, greater number (30 or more) along inner edge, in two rows. Dorsal parameres yellowish brown near base, paling to translucent yellowish near tips, with lightly sclerotized apical appendage bent back toward base of aedeagus. Ventral valves yellowish brown, with thin ridge extending along either side of notch containing small, pale dorsal valves and merging with bases of dorsal parameres. Aedeagal hamulus absent, but broadly V-shaped, sclerotized band connecting ventral parameres somewhat thickened medially. Segments 10 and 11 often protruding ventrad between dististyles; cerci inconspicuous.

Abdomen of female. Terga and sterna unevenly dark yellowish brown to brown, with short, yellow setae. Subgenital plate (Fig. 83) wide and long, apex acute to narrowly rounded (allotype); longest marginal setae about one-fourth greatest width of plate, 6 to 8 along each side, 4-6 on underside shortly before apex. No laterotergites, but cuticle near base of subgenital plate continuous with sclerotized folds partially enclosing genital plates. Apical and basal genital plates of about same width (Figs. 84, 85); axial portion not extending to posterior margin; apodemes moderately divergent.

Body length, male, about 9.5 to 13 mm. (holotype 12 mm.); female, about 9-12 mm. (allotype 11 mm.). Length of fore wing, male, 10.0 to 12.8 mm. (holotype 11.6 mm.); female, 10.3 to 12.4 mm. (allotype 11.5 mm.). In general, females are smaller than males, and spring males are slightly larger than autumnal ones.

Holotype male and allotype (mating pair) collected 8 miles west of Greensboro, in the Oconee National Forest, Greene Co., Georgia, 1 October 1977, G. W. Byers (field cat. Greene Co. no. 1). Paratypes: GEORGIA: Baldwin Co., 1 mi. E of Milledgeville,

15 Sept. 1990, WB (1m); Banks Co., 1 mi. W of Homer, 1 Sept. 1991, WB (5m); Clarke Co., Athens, N. Oconee River, 2 Oct. 1977, GWB (1m, 3f); Clarke Co., Athens, 27 Apr., 16 & 17 May, 20-26 May in Malaise trap), -July (6m); Greene Co., same data as holotype (3m, 3f); same, but 3 Oct. 1977, GWB (6m, 3f); Greene Co., along Oconee River, Oconee National Forest, 3 Oct. 1977, GWB (1m); Greene Co., 14 Sept. 1980, WB (1m); Gwinnett Co., 3 mi. W of Loganville, 3-4 May 1980, WB (3m); same, but 14 Sept. 1980, WB (1m); Hall Co., 1 Sept. 1991, WB (1m, 1f); Henry Co., in sticky trap, June 1978, W. Morrill (2m, 3f); Jackson Co., 10 mi. NW of Jefferson, beside U.S. hwy. 129, 28 May 1978, GWB and C. W. Young (4m); Jackson Co., 1 mi. E of Commerce, 16 Sept. 1990, WB (1m); Madison Co., NW of Neese, 2 Sept. 1976, C. K. Starr (1m); Morgan Co., 11 mi. W of Madison, 1 Oct. 1977, GWB (1f); Morgan Co., Hard Labor Creek State Park, 31 Aug. 1984, WB (2m); Oconee Co., N edge Oconee Nat. Forest, 5 and 15 Sept. 1980, WB (2m); Oglethorpe Co., 3 mi. SE of Lexington, 4 Oct. 1977, GWB (1m); Oglethorpe Co., hwy. 22 1 mi. S of Little Creek, 15 Sept. 1990, WB (2m); Rockdale Co., 28 April 1991, WB (3m, 1f); Taliaferro Co., 2 mi. S of Lyneville, 15 Sept. 1990, WB (2m).

Holotype, allotype and most paratypes are in the SEM; 8 paratypes in WB collection; paratypes also deposited in the USNM and MCZ.

Panorpa acuminata closely resembles *P. rupeculana* and *P. pachymera* in both structure and color. Its known range is adjacent to that of *pachymera*, and the two ranges meet in Baldwin and Taliaferro counties, Georgia. *P. acuminata* differs from *pachymera* most noticeably in the males' ventral parameres, which are longer but more slender than those of *pachymera*, are not bowed ventrad (except slightly at base of free portion), have more numerous and thinner barbs and have the acuminate, sclerotized tip extending as far as or (usually) beyond the longest terminal barbs (Fig. 82). The ventral parameres are long and slender in the similar *P. robusta* but in that species are bowed ventrad (or laterad, depending on postmortem drying) and bear much shorter, more slender barbs not in perceptible rows. The most similar ventral parameres are in *P. rupeculana*, but males of that species have four thick, black setae on each basistyle, as well as other differences (see *P. rupeculana*).

Panorpa acuminata takes its name from the ventral parameres of the male (Latin *acuminata* = tapered to a slender point).

The holotype, allotype and several paratypes were collected from the upper leaves of clumps of honeysuckle 2-3 feet high, in a woods of pine, oaks, red gum, hickory and dogwood. While honeysuckle was abundant at this site, its usual ecological associates in the Southeast, namely, brambles and greenbriars, were only occasional or rare; and poison ivy was less common than in most such situations, occurring in scattered, limited areas where woodbine (Virginia creeper) was equally abundant. The initial collection at the type locality was made after sunset (6:50-7:25 EDST). Under twilight but hot (84°F.) and humid conditions, males of both *P. acuminata* and *P. oconee* were "calling." That is, they held their wings somewhat outspread and the genital bulb as high as possible, the position associated with dispersal of sex-attractant pheromone.

How this species and the similar *P. pachymera* are related remains to be studied. The two forms are generally geographically separated and are consistent in structure within their respective ranges. Individuals with intermediate characteristics have not been found.

Panorpa rupeculana new species

Description based on 9 males, 4 females, pinned.

Head: Dorsum, frons and rostrum amber brown except black ring around each ocellus; mouthparts amber brown, tips of apical segments of maxillary palps darker brown. Scape, pedicel and basal two-thirds of first flagellomere yellowish brown; flagellum blackish brown, with 38 flagellomeres in both male and female.

Thorax: Dorsum unevenly brown (some mottling clearly due to post-mortem changes) without markings; pleural surfaces, coxae and mera unevenly light brown with fine whitish to silvery pubescence on mesothorax and metathorax, scattered yellowish setae longest and most numerous on anterior surfaces of coxae; a few black setae on anterior surfaces of middle coxae and apical edges of hind coxae. Legs yellowish brown, tibiae somewhat paler than femora; tarsi darker, brown on tarsomeres 4 and 5.

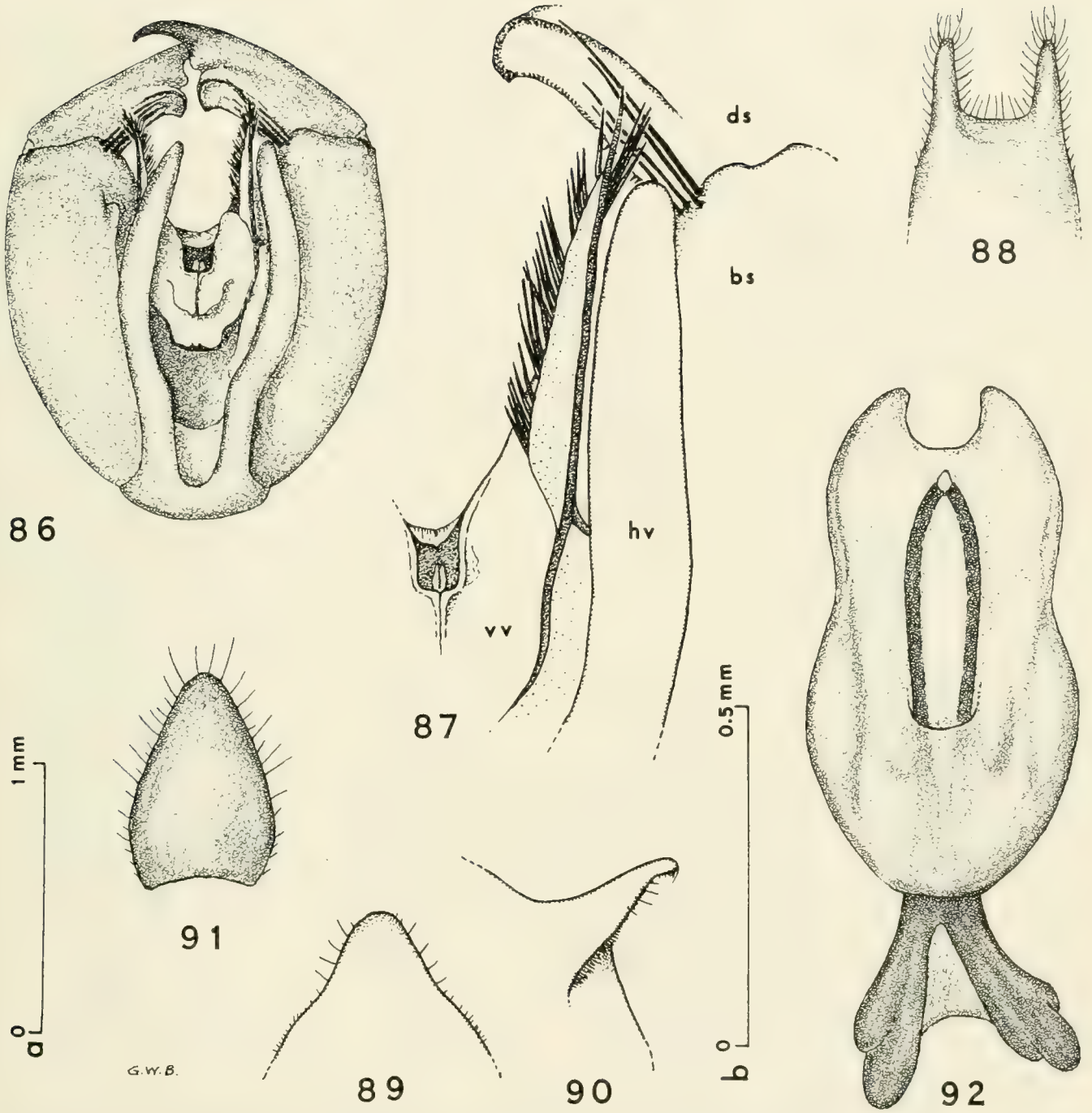
Wings tinged with yellowish brown, bands and spots brown to dark brown. Apical band complete but including marginal pale band from R_3 to behind M_1 in both sexes, pale area less extensive to absent in hind wings. Pterostigmal band complete, slightly narrowed behind M_{1+2}, unbranched but with outer branch suggested by spot at margin between M_3 and M_4 (holotype), extending to M_2 in female. Marginal spot from C to behind R_{4+5}, surrounding nygma (holotype), interrupted between R_{2+3} and R_{4+5} in other specimens. Basal band interrupted near mid-length, approximately M to Cu_1. Basal spot from R or M to Cu_2. First humeral spot from C to R, slightly beyond h.

Abdomen of male: In dried specimen, terga and sterna 2-6 unevenly sordid brown, dark yellowish brown in life, segments 7 and 8 more evenly dark amber brown, genital bulb amber brown; in holotype, tergal horn broad at base in dorsal aspect (narrower in paratype), slender in lateral aspect (Figs. 89, 90). Notal organ slightly developed: posterior margin of tergum 3 not noticeably produced, hairs decurved but neither thickened nor darkened; thick peg on anterior tergum 4 (barely visible in posterior aspect in holotype). Genital bulb (Fig. 86) about as wide as its length measured to ends of basistyles. Hypovalves deeply separated, of nearly uniform width throughout, narrowed only slightly near apex, with about 18 long setae along mesal margin and at apex of each, some setae twice as long as width of hypovalve. Tergum 9 (Fig. 88) with broadly U-shaped emargination between slender lobes (finger-like in dorsal aspect but flattened), each bearing loose tuft of yellowish hairs apically. Dististyles slightly convex on outer surface of basal two-thirds, then narrowing and curving evenly to acute apex; inner basal cup with narrow, darkly sclerotized margin, except toward base, margin slightly thickened at dorso-mesal angle; dorsal margin with six (or more) short, thick, black, acutely tipped setae. Ventro-mesal apex of each basistyle bearing four long, thick, black setae extending far into cup of dististyle. Ventral parameres (Fig. 87) also extending to cups of dististyles, or farther, overlapping thick setae of basistyles (tips bent dorsad in paratype); only four or five subapical barbs on outer side, about five times as many along mesal side, attached to long-triangular membranous margin; sclerotized band of paramere tapering to acute tip slightly beyond terminal barbs. Dorsal parameres slender, largely concealed by ventral parameres in ventral aspect, yellowish brown at base just above fusion with ventral valves, brown around dorsal valves, translucent yellowish apically, with small dorsal appendage bent back toward base of aedeagus. Ventral valves pale yellowish brown, semimembranous; dorsal valves small, pale. No aedeagal hamulus, but sclerotized band connecting ventral parameres slightly widened near mid-line. Segments 10 and 11 small, extending slightly between dististyles. Cerci small, concealed beneath ninth tergum.

Abdomen of female: Terga and sterna yellowish brown in life; in dried specimen unevenly brown to dark brown; cerci black. Subgenital plate (Fig. 91) subtriangular, narrowly rounded at apex, widest just beyond base. Genital plates (Fig. 92) with short posterior lobes separated by U-shaped notch; outer margins of lobes evenly rounded; basal plate slightly wider than apical plate; axial portion not attaining posterior margin; apodemes thick, moderately divergent (left one bent ventrad in allotype).

Body length, male, 9.1-11.5 mm. (holotype, 11.4 mm.); female, 8.6-10.3 mm. (allotype 10.3 mm.). Length of front wing, male, 10.3-11.6 mm. (holotype, 11.0 mm.); female, 10.6-11.8 mm. (allotype 10.6 mm.).

Holotype male and allotype female, at roadside park (Burns Park) on highway I-40, 7 miles NW of center of Little Rock, Pulaski Co., Arkansas, 22 September 1977, George W. Byers (field cat. no. 1). The park is on both sides of the highway, at the western edge of



Figs. 86-92. *Panorpa rupeculana*, n. sp. **86,** genital bulb, male holotype, ventral aspect (most hairs omitted). **87,** right ventral paramere and associated structures, holotype (bs - apex of basistyle, ds - basal portion of dististyle, hv - right hypovalve, vv - ventral valve of aedeagus). **88,** ninth abdominal tergum, holotype. **89,** tergal horn of sixth abdominal segment, dorsal aspect. **90,** same, left lateral aspect. **91,** subgenital plate, female allotype, ventral aspect. **92,** genital plate, allotype, ventral aspect. Scale a, figs. 86, 88-91; scale b, figs. 87, 92.

North Little Rock. Paratypes: ARKANSAS: Ouachita Co., 8.7 mi. NE of Camden, 24 Oct. 1957, I. J. Cantrall, T. Cohn, D. Eades (1m). LOUISIANA: Morehouse Parish, 13 Sept. 1992, WB (1m). MISSISSIPPI: Choctaw Co., 6 Sept. 1986, WB (1m); Lafayette Co., Puskus Lake, 8 mi. NE Oxford, 23 May 1978, GWB and C. W. Young (1m); Pontotoc Co., 13 Sept. 1992, WB (1m, 3f); Tishomingo Co., 25 May 1986, WB (1m); Webster Co., milepost 211 Natchez Trace Parkway, 6 Sept. 1986, WB (2m).

Holotype, allotype and one paratype are in the SEM; paratypes in the UMMZ, and collection of Wes Bicha.

Panorpa rupeculana at once recalls *P. acuminata* because the ventral parameres in males of both species are long and end in a slender, sharp point. The former, however, has four thick, black setae on each basistyle, while *acuminata* ordinarily has none, or occasionally one or two. The membranous portion of the paramere to which the outer terminal barbs are attached, in *acuminata*, is not present in *rupeculana*. Less apically tapered hypovalves and less conspicuous dorsal parameres in *rupeculana* are other readily noticeable differences. Females of this species differ from those of others in the *rufescens* group by the relatively short posterior lobes on the apical genital plate, as well as by the over-all shapes of the genital plate and subgenital plate. That the known ranges of *rupeculana* and *acuminata* are separated by some 240 miles, or 385 km., the area between having been searched for scorpion-flies, influenced my opinion that the Arkansas specimens represent a separate species.

The name of the species is derived from Latin *rupecula*, the diminutive of *rupes*, a rock (in the sense of a crag or rock cliff, such as the outcrop on the south bank of the Arkansas River from which the city of Little Rock takes its name).

At the type locality, *Panorpa rupeculana* and *P. nuptialis* were found in a small, shaded area about 50 by 20 feet of tangled greenbriar, honeysuckle, brambles, goldenrod, etc., in a woods of oak, hickory, maple, red gum, pine and other trees, in the southwestern part of the park, near the Arkansas River.

Panorpa venosa Westwood

In an earlier paper (Byers, 1962b: 473-474, Fig. 2), I synonymized *P. venosa* with *Panorpa rufescens* Rambur. As explained above under *rufescens*, however, the lectotype of *rufescens* was incorrectly chosen, as apparently it was not one of Rambur's original series; and the name *rufescens* is now limited to a species essentially of northeastern United States. The female lectotype of *P. venosa* (one of two female syntypes, the other now lacking the posterior parts of the abdomen) was collected at some unspecified locality in Georgia. Since, as shown above, there are no fewer than four species of the *rufescens* group that might be expected in Georgia, it became important to examine the genital plates of the lectotype of *venosa* to determine to which form the name should now be applied.

I began with the assumption, possibly incorrect, that a specimen collected in Georgia in the early 1840's or some time prior to that is likely to have been found in the environs of Savannah. The first European settlement in Georgia, Savannah was the early administrative center of the state, and for some decades it was the cultural capital as well. On the basis of geographical position and wing markings (mainly the number and extent of clear areas included within the apical band), specimens collected on Sapelo Island, about 40 miles (64 km.) south of Savannah seemed the most likely to be conspecific with *venosa*. No specimens were available from anywhere nearer Savannah.

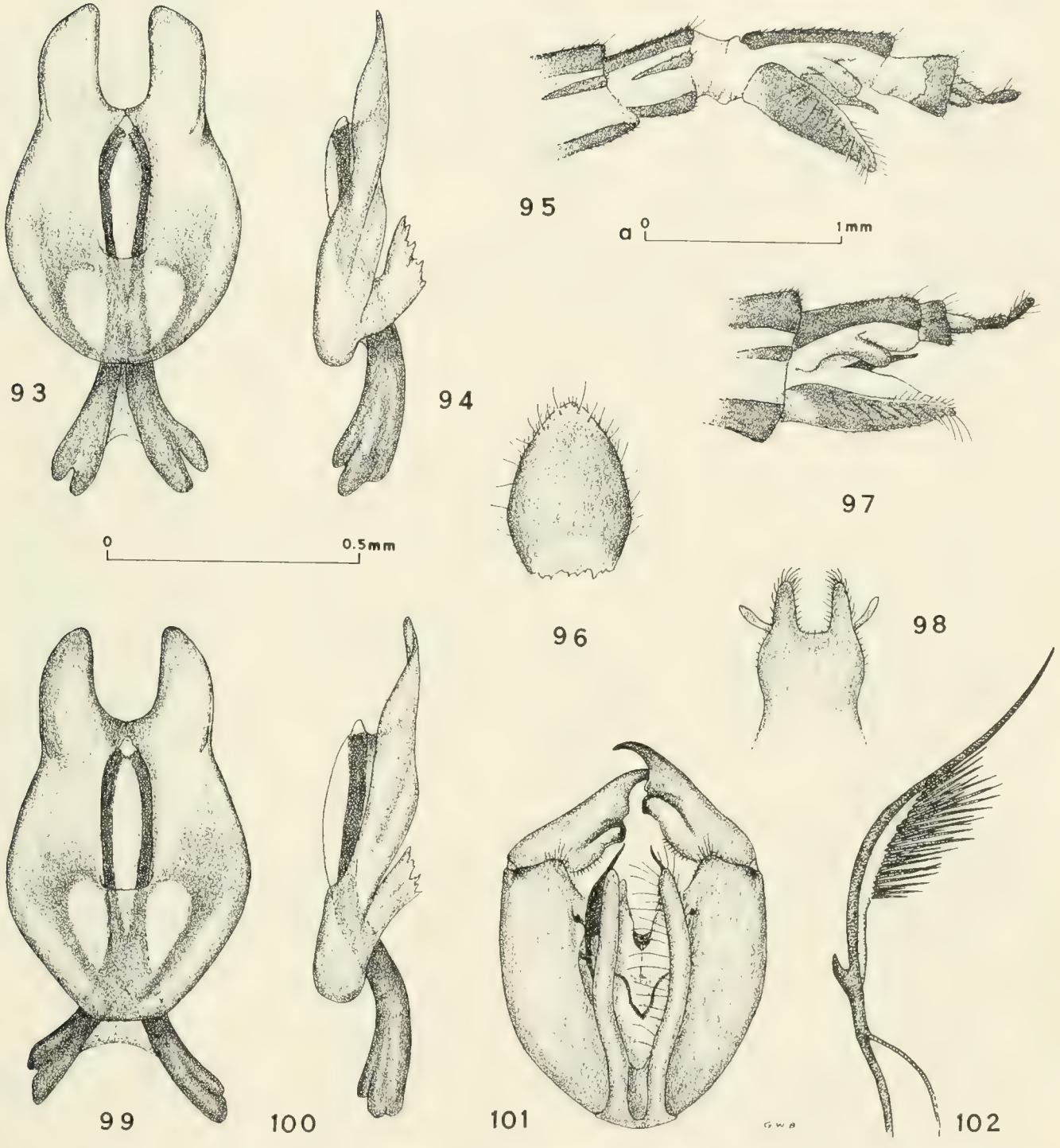
Dr. Stephen J. Brooks of the Natural History Museum, London, kindly removed the posterior segments of the lectotype of *P. venosa* and sent these to me, with permission to make the necessary dissection. The small, smoothly rounded laterotergites beside the ninth abdominal tergum (Fig. 95) somewhat resemble those of *planicola* (Fig. 104) from coastal South Carolina but are smaller and more diagonal in position with respect to the tergum. The subgenital plate of *venosa* (Fig. 96) has the shape seen in more than one other species and is pale apically as in some others, but it also has a broad, almost semicircular basal area without setae. The lateral and dorsal marginal setae (Fig. 95) are much the same as in *planicola*. The genital plate of females from the population on Sapelo Island (Figs. 99, 100) agrees with that of the lectotype of *venosa* except in minor details that, in my opinion, fall easily within the range of intraspecific variation based on that seen in females of other species. At each side of the axial portion of the plate, there is an area of thin, translucent cuticle bordered laterally by a darker zone that fans out posteriorly (this due in part to more densely sclerotized structures on the dorsal side of the basal plate). In addition, there is a rather abrupt narrowing of the apical plate beyond the indistinct end of the basal plate. These characteristics are shared with *P. planicola* (Figs. 105, 106), but in that species the posterior lobes of the apical plate are shorter and wider.

Males of *Panorpa venosa* (Figs. 101, 102) possess many characteristics of the *rufescens* group but most closely resemble those of the more inland *P. acuminata* of north-central Georgia. As in that species, the genital bulb is about as wide as its length excluding the dististyles, the basistyles lack thick, black apical setae (which are sometimes present in *acuminata*) and the ventral parameres are prolonged beyond the ends of the terminal barbs. In details of the ventral parameres, however, *venosa* is conspicuously unlike any other species of the *rufescens* group. The apical 30 per cent of the free part of the ventral paramere has no barbs (Fig. 102), while the more basal portion bears numerous long barbs along its mesal edge. (In a male pinned from alcohol, the ventral parameres twisted in drying, making the barbs somewhat dorsal but still readily visible.) The sclerotized band connecting the ventral parameres is slender, its medial portion nearly V-shaped; and the basistylar flanges are small and bluntly rounded.

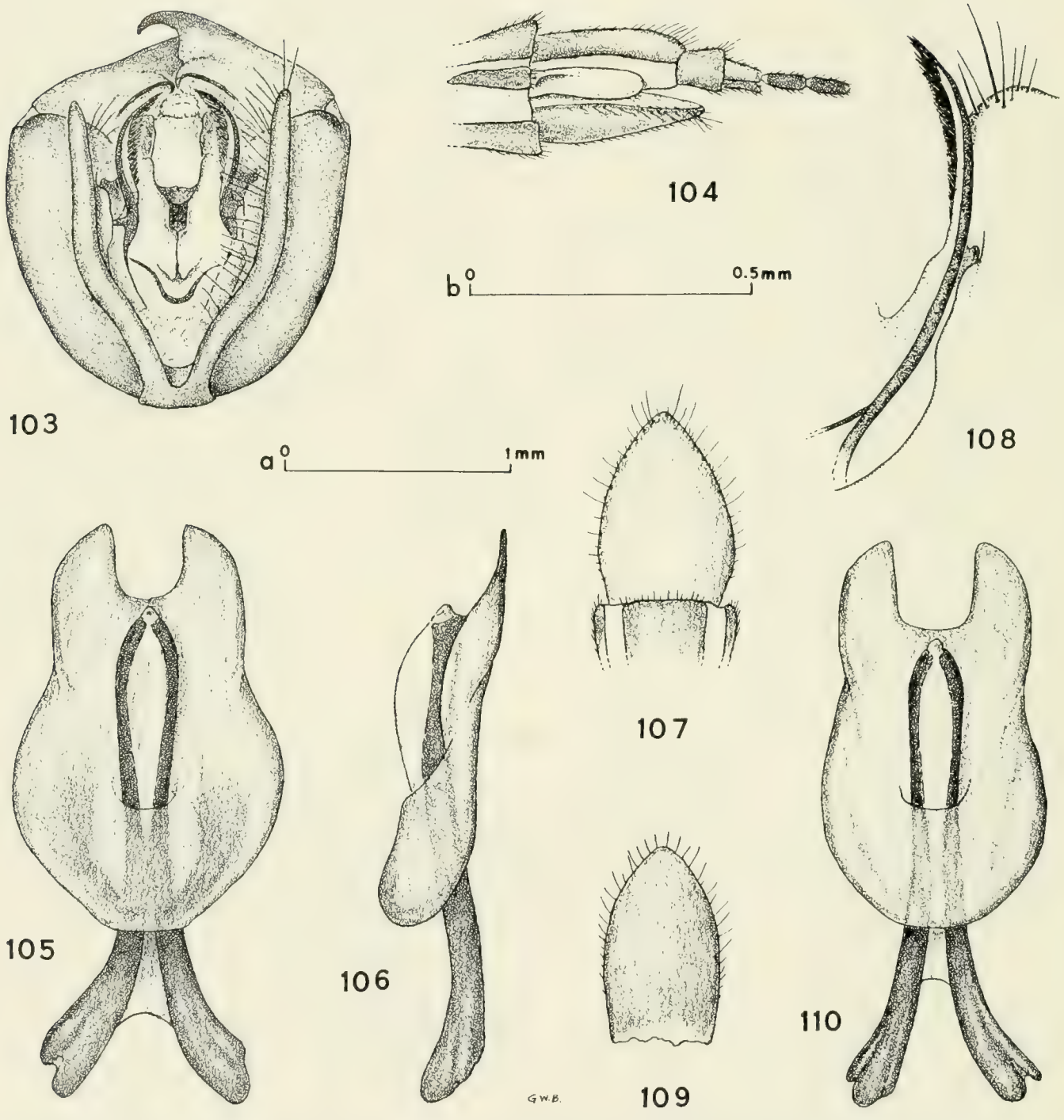
Association of males with females that agree in detail with the lectotype of *P. venosa* has only recently been possible, thanks to the cooperation of Dr. Stephen Brooks already mentioned and Dr.Laurent LeSage of Agriculture Canada, who sent the following specimens for identification: GEORGIA, McIntosh Co., Sapelo Island, pan trap in live oak forest, 28 April-9 May 1987, Biosystematics Research Centre, Hymenoptera team (2m, 3f); same except 9-25 May 1987 (2m, 4f); same locality, etc., but collected by flight-intercept trap, 29 May-20 June 1987 (3f); same but in flight-intercept trap in savanna, 29 May-20 June 1987 (1f); same locality but collected from herbaceous growth in oak forest, 29 April 1987, H. Goulet (1m).

Panorpa vernalis Byers

Named *vernalis* because no other *Panorpa* had been taken in early spring in Mississippi (although *anomala* Carpenter was found at the same time as *vernalis*), this species is now known to have an autumnal emergence of adults. On 23 September 1977, I returned to the type locality in Claiborne Co., suspecting there might be a fall generation, and found, in a short time, three males and one female, as well as a few individuals of *anomala*. More recently, I have seen a specimen from East Baton Rouge Parish, Louisiana, collected on 13 November. The species is also known from southern Arkansas, in spring.



Figs. 93-96. *Panorpa venosa* Westwood, female lectotype. **93,** genital plate, ventral aspect. **94,** same, right lateral aspect. **95,** terminal abdominal segments (7-11), left lateral aspect (extension due to maceration in KOH). **96,** subgenital plate, ventral aspect. **Figs. 97-102.** Specimens from Sapelo Island, Georgia, judged to be *Panorpa venosa*. **97,** terminal abdominal segments, female, left lateral aspect. **98,** ninth abdominal tergum, male. **99,** genital plate, female, ventral aspect. **100,** same, right lateral aspect. **101,** genital bulb, male, ventral aspect. **102,** left ventral paramere, male, ventral aspect. Scale a, figs. 95-98, 101; scale b, figs. 93-94, 99-100, 102.



Figs. 103-107. *Panorpa planicola*, n. sp. **103,** genital bulb, male holotype, ventral aspect. **104,** terminal abdominal segments, female allotype, left lateral aspect. **105,** genital plate, allotype, ventral aspect. **106,** same, right lateral aspect. **107,** subgenital plate, allotype, ventral aspect. **Figs. 108-110.** *Panorpa robusta* Carpenter. **108,** right ventral paramere, male holotype, ventromesal aspect. **109,** subgenital plate, female from Darlington Co., South Carolina. **110,** same female, genital plate, ventral aspect. Scale a, figs. 103-104, 107, 109; scale b, figs. 105-106, 108, 110.

Panorpa planicola new species

Description based on five males, one female, pinned but originally preserved in alcohol.

Head: Dorsum, frons and rostrum, including palps, dark yellowish brown, except apical half of terminal segment of maxillary palps blackish brown and blackened crescent above each ocellus. Scape, pedicel and most of basal flagellomere dark yellowish brown; flagellum blackish brown, with 37 to 39 flagellomeres (holotpype 38).

Thorax: Dorsum sordid yellowish brown, without pattern; pleural surfaces, coxae and mera dull yellowish brown, finely pubescent except small glabrous area beneath each wing base, with scattered pale setae and a few darker setae on anterior surfaces of fore and middle coxae. Legs and tarsi yellowish brown with dark setae; fifth tarsomere darkened apically.

Wings tinged with yellowish brown, bands and spots brown. Apical band including several pale spots, in males, one or two in female. Stigma pale, dull yellow (possibly an artifact of initial preservation), except portion covered by pterostigmal band. Pterostigmal band entire but narrow near mid-length, unbranched, with pale spot included at end of Sc in holotype. Marginal spot present, usually from C to slightly behind R_1 (stops at R_{2+3} in holotype); also spots over cross-vein from R_1 to R_{2+3} and behind R_{4+5}; all cross-veins darkly bordered. Basal band of two spots separated between M and Cu_1. First basal and first humeral spots present, latter extending to R_1.

Abdomen of male: Terga 1-5 unevenly sordid yellowish brown, corresponding sterna slightly paler; segment 6 more evenly dark yellowish brown, with blunt-tipped tergal horn; segments 7-8 yellowish brown, 9 slightly darker. Notal organ a broad, scarcely protruding lobe with downcurved black setae, on third tergum, and a blunt peg on anterior fourth tergum. Genital bulb (Fig. 103) about as wide as its length measured to ends of basistyles. Hypovalves (unnaturally divergent in holotype, although degree of divergence near bases is about as shown) slender, narrow near base then widening slightly for most of length but narrowing again toward apex, extending to or a little beyond ends of basistyles; 6-12 long setae twice width of hypovalve on mesal margin and at apex, other setae shorter. Tergum 9 with two slender, subparallel apical lobes, emargination between them U-shaped. Cerci inconspicuous in most males, concealed by tergum in holotype. Basistyles without blackened, thick apical setae; flange on inner, ventral surface narrow (low), edge nearly straight (holotype) or broadly rounded. Dististyles with shallow inner basal cup bordered by dark brown, strongly sclerotized ridge with dorso-mesal angle, or tooth; row of short, sharply tipped, black setae along dorsal edge of cup near base. Ventral parameres nearly straight, extending beyond ends of basistyles, somewhat flattened, with darkly sclerotized outer edge and shorter, paler inner edge, latter densely set with short, thin barbs increasing in length toward apex of paramere; barbs not in evident rows, longer apical ones extending into cups of dististyles in preserved specimens. Dorsal parameres sclerotized and brown beyond basal fusion with paler ventral valves. Dorsal valves pale, inconspicuous, in notch between darkened inner bases of dorsal parameres. No aedeagal hamulus.

Abdomen of female: All terga and sterna unevenly sordid yellowish brown, sterna slightly paler than terga. Cerci black, their membranous parts white. Subgenital plate (Fig. 107) pointed at apex, only slightly narrowed basally, with evenly dispersed short setae but longer setae on lateral margins and at apex. Laterotergites of ninth segment elongate, rounded posteriorly, pale yellowish brown (Fig. 104). Genital plates (Figs. 105, 106) with posterior lobes broad, emargination between them U-shaped; axial portion not extending to margin of apical plate; apodemes divergent, thick at tips; basal plate thick medially beneath axial portion.

Body length, male, about 10 to 11 mm (holotype approximately 11 mm; abdomen strongly flexed at end of sixth segment); female (allotype) about 11.5 mm. Length of fore wing, male, 10.5 to 11.7 mm (holotype 11.7 mm); female, 12.1 mm.

Holotype male, from Edisto Island, Charleston Co., South Carolina, 29 Oct. 1988, collected by Wes Bicha. Allotype, Givhans Ferry State Park, Dorchester Co., South Carolina, 8 Oct. 1988, WB. Paratypes, all from South Carolina: Edisto Island, Charleston Co., 29 Oct. 1988, WB (3m); Givhans Ferry, Dorchester Co., 28 May 1988, WB (1m).

Holotype, allotype and one paratype in the SEM; other paratypes in collection of Wes Bicha.

This species resembles *P. hispida* and *P. scopulifera* in many details. Males differ from those of *hispida* and *scopulifera* most noticeably in lacking thick, black setae on the inner, ventral apices of the basistyles and in the structure of the ventral parameres. In *planicola*, the barbs are very numerous, mostly short and slender and not in distinct rows along the inner surface of the ventral parameres. *Panorpa hispida*, the range of which contacts that of *planicola*, has fewer and much longer, wider barbs on more curved ventral parameres, and the barbs appear to be in a narrow row on the inner edge of each paramere. In females, the laterotergites of the ninth abdominal segment are similarly pale, swollen, smoothly rounded apically (posteriorly) and elongate in *planicola*, *hispida* and *scopulifera* but are thicker anteriorly in *planicola* than in the other two. There are also evident differences in the shapes of the genital plates (compare figures 47-48, 52-53 and 105-106).

The species takes its name from its general habitat on the coastal plain (Latin *planus*, a plain or flatland, and *colo*, dwell, inhabit). Mr. Bicha reports that *P. planicola* was associated with dense growths of honeysuckle at both localities from which it is known. (Since the honeysuckle was introduced from eastern Asia, one wonders what plant association comprised the native habitat of so many regional species of *Panorpa* that have been found on honeysuckle.) On Edisto Island, the honeysuckle was growing beneath live oaks festooned with Spanish moss (*Dendropogon usneoides*).

Panorpa robusta Carpenter

Described from a single male (Carpenter, 1931:240), this species has remained something of a puzzle. The holotype was from Meredith, South Carolina, a village that ceased to exist some time about 1930 but was near the present town of Manville, in Lee County. Carpenter (1939:164) subsequently reported two males from Dacula (Gwinnett Co.), Georgia. The female has not been described.

In *robusta*, the ventral parameres are the best recognition character, as in males of all species of the *rufescens* group. In the holotype and most other males, these parameres are oriented so that the numerous short, slender barbs are primarily on the dorsal surface, all but concealed in ventral aspect. In ventro-mesal aspect, however, their abundance and distribution can be seen (Fig. 108). The only other named regional species known to me that has so many short, thin barbs not in distinct vertical or longitudinal rows is *P. ensigera* Bicha (1983) from North Carolina. This species differs from *robusta* in having three thick, black setae on the ventro-mesal apex of each basistyle.

In external appearance, the female of *robusta* resembles that of *P. scopulifera*, particularly in the shape of the subgenital plate (Fig. 109; cf. Fig. 50), but it lacks the conspicuous laterotergites of *scopulifera*. The genital plates in *robusta* (Fig. 110) are shorter in comparison to their anterior apodemes, the distal lobes of the apical plate are more widely separated, the emargination being broadly U-shaped, and the medial part of the basal plate has quite a different shape in the two species.

The only series of *Panorpa robusta* I have seen (5m, 10f) was collected in Darlington Co., South Carolina, near Hartsville, on 26 September 1930, by T. H. Hubbell (his field cat. no. 29). This place

is only 20 miles (32 km) northeast of the type locality. On the same day, Prof. Hubbell collected an additional male in Florence Co., near Scranton. Wes Bicha returned to this area in 1992 and found two males, one female in Darlington Co. (16 Oct.) and one male in Florence Co. (17 Oct.); and his son Fred Bicha collected one male in Williamsburg Co. on 18 Oct. Earlier Wes Bicha had found one male in Dorchester Co., on 8 October 1988, and another on 29 October 1988, near U.S. hwy. Alt. 17, 2 mi. E of county line (Edisto River). In the USNM there is a male from Charleston Co., South Carolina, dated "IX.20", from the G. M. Greene collection.

Panorpa ensigera Bicha

Distinctly bivoltine, this species has been found from late May to mid-June and again in September and October. Bicha (1983) originally recorded *ensigera* from Richmond Co., North Carolina, 16 Sept. 1980 and 12-13 June 1981, and from Moore Co., N.C., 16 Sept. 1980. More recently, he has collected truly autumnal specimens of *ensigera* in Lee Co., N.C., 27 Sept. 1986, and Scotland Co., N.C., 15 Oct. 1984 (also 29 May 1988).

UNUSUAL AUTUMNAL RECORDS

There are a few common species with extensive spring-summer periods of emergence for which there are occasional autumnal records. These autumnal occurrences probably represent individuals of late-summer generations that were somehow developmentally delayed, or late-summer weather may have been prolonged in certain years or at particular places. Following are such unusual autumnal records of adult Mecoptera in the Southeast.

Panorpa anomala Carpenter

Most of the geographic range of this species is north of the area under consideration, in Iowa, Wisconsin, Illinois and Michigan; and most date records indicate spring and late summer appearances of the adults, even in Arkansas, Missouri and Mississippi. However, I found *P. anomala* together with *P. vernalis* at Rocky Springs Park, on the Natchez Trace Parkway, Claiborne Co., Mississippi, on 23 September 1977. And I have seen a female specimen from East Baton Rouge Parish, Louisiana, collected on 6 November 1982.

Panorpa insolens Carpenter

Kentucky: Clark Co., Winchester, 15 Oct. 1960 (1f); Fayette Co., 7 Oct. 1954 (1f); Jefferson Co., near Louisville, 7 Oct. 1976 (1m); Knox Co., 11 Oct. 1941 (1f, not dissected, could be *P. helena*); Oldham Co., 21 Sept. 1971 (1m); Rowan Co., Morehead, 16 Oct. 1965 (1f).

Panorpa longicornis Carpenter

North Carolina, Jackson Co. (on Macon Co. line), Whiteside Mountain, 22 Sept. 1937 (1m).

Panorpa nebulosa Westwood

Missouri, Boone Co., near Columbia, 10 Oct. 1953 (1m).

Panorpa speciosa Carpenter

Kentucky, Jefferson Co., Louisville vicinity, 7 Oct. 1976 (1f).

KEY TO AUTUMNAL MECOPTERA OF SOUTHEASTERN UNITED STATES

1. Tarsi with a single, large claw (Family Bittacidae) 2
—Tarsi each with two small claws 3
2. Cross-vein between Sc and R_1 beyond level of first fork of Rs; lobes of tergum 9 of male only slightly longer than basistyles; cerci about half as long as basistyles ..... *Bittacus occidentis*
—Cross-vein between Sc and R_1 before level of first fork of Rs; lobes of tergum 9 of male more than twice as long as basistyles; cerci much longer than basistyles ..... *Bittacus texanus*
3. Costal cell of fore wing with ten or more cross-veins beyond humeral cross-vein; body slightly depressed; head strongly opisthognathous (Family Meropeidae) ..... *Merope tuber*
—Costal cell without cross-veins beyond humeral cross-vein; body not depressed; head prolonged ventrad as a rostrum, hypognathous (Family Panorpidae, genus *Panorpa*) 4
4. Hypovalves of sternum 9 of male less than one-third length of genital bulb excluding dististyles and borne on prolongation of sternum on ventral surface of bulb; tergum 9 narrowed toward subacute apex, without posterior lobes; genital plates of female without posterior lobes on apical plate, axial portion thick, its apodemes only slightly divergent (*lugubris* group) 5
—Hypovalves of sternum 9 deeply separated, from two-thirds as long as genital bulb to slightly exceeding ends of basistyles; tergum 9 with two posterior lobes (broadly truncate in one regional, montane species not of autumnal occurrence); apical genital plate of female with two narrow to wide posterior lobes, axial portion usually less than one-third width of plates, with moderately to widely divergent apodemes 8
5. Wings mostly black, with few small, white spots ..... *P. lugubris*
—Wings tinged with yellowish brown, bands and spots brown 6
6. Wings lightly tinged with yellowish brown; pterostigmal band diagonal, unbranched; basal band strongly constricted at M; humeral area of wing clear, without humeral spots ..... *P. floridana*
—Wings strongly tinged with yellowish brown; pterostigmal band branched or, if unbranched, wide; basal band rarely constricted near mid-length; humeral area of wing darkened, pigmented area connected to first basal spot 7
7. Dark band along posterior margin of wing from basal band to wing base; pterostigmal band broad, not branched ..... *P. nuptialis*
—Dark band along anterior edge of wing from basal band to wing base; pterostigmal band usually branched, its outer or distal branch often joining apical band near wing margin ..... *P. rufa*
8. Inner basal cups of dististyles of male directed more or less mesad, deep, with wide flange-like borders; hypovalves slender, extending to ends of basistyles or farther (cf. *longicornis*); ventral parameres nearly straight, extending between dististyles; aedeagal hamulus conspicuous, blunt-tipped; basal plate of female genital plates narrower than apical plate; laterotergites strongly sclerotized, their outer surfaces convoluted (*virginica* group) 9
—Inner basal cups of dististyles shallow, without wide flange-like borders, directed basad or ventrad; hypovalves of variable length; ventral parameres not reaching beyond cups of dististyles, or, if longer, strongly curved (except in *longicornis*); basal plate of female genital plates as wide as or wider than apical (distal) plate; laterotergites, if present, only moderately sclerotized, their outer surfaces smooth (or longitudinally folded in dried specimens) 12
9. Ventral parameres stout and long, extending beyond ends of dististyles, often in contact in apical one-third (Fig. 17); ventral margin of inner basal cup of dististyle prolonged mesad as two prominent points, basal one longer than wide; distal one less narrow; laterotergites of female expanded ventrally beneath sides of subgenital plate (Fig. 21); axial portion of genital plates only slightly prolonged cephalad from basal plate (Fig. 22) ..... *P. choctaw*
—Ventral parameres extending only to ends of dististyles, or shorter, apical ends well apart; ventral margin of cup of dististyle irregular (jagged) or with projections about as wide as their length; laterotergites as in *choctaw* or altogether lateral; axial portion of genital plates prolonged cephalad more than half length of plates alone 10
10. Ventral parameres of male extending only into basal cups of dististyles (Fig. 11) ..... *P. neglecta*
—Ventral parameres extending to tips of dististyles 11
11. Ventral margin of cup of dististyle smooth; angular projections about as wide as long (Fig. 13) ..... *P. oconee*
—Ventral margin of cup jagged; angular projections wider than long ..... *P. virginica*
12. Wings strongly tinged with yellow to yellowish brown, with three broad, transverse, dark brown bands (apical, unbranched pterostigmal, uninterrupted basal bands, width of each at mid-length equal to 10% or more of wing length), a small marginal spot, and joined first basal and first humeral spots ..... *P. americana*
—Wing membrane colorless to tinged with yellowish brown; bands and spots brown to dark brown; bands, if present, narrower with irregular edges; basal band often interrupted near mid-length; first basal and first humeral spots not joined 13

13. Sixth abdominal segment of male without posterodorsal horn; wings with spots only (no bands), pterostigmal spot often roughly triangular; axial portion of genital plates of female protruding beyond posterior margin of apical plate, apodemes large, widely divergent ..... *P. nebulosa*
—Sixth abdominal segment of male with posterodorsal horn; wings with bands and spots or spots only, pterostigmal spot not triangular; axial portion of female genital plates not reaching posterior margin of apical plate, apodemes variable 14
14. Dististyles of male with subrectangular projection on ventral surface near base; ventral parameres slender, extending to tips of dististyles or beyond; pterostigmal band branched; apical genital plate of female with slender posterior lobes curved mesad; no apodemes projecting cephalad from basal plate ..... *P. longicornis*
—Dististyles of male without rectangular projection from ventral surface; ventral parameres not extending to tips of dististyles; genital plates of female usually with projecting anterior apodemes, if not, pterostigmal band interrupted, incomplete; posterior lobes of apical (distal) plate wide 15
15. Aedeagal hamulus present, in male; ventral parameres extending beyond basal cups to mid-length of dististyles; posterior lobes of distal plate in female more than twice as long as their basal width, space between them as wide as deep 16
—Aedeagal hamulus absent, in male; ventral parameres short, not reaching beyond basal cups of dististyles; posterior lobes of distal plate in female about twice as long as their basal width, or less, space between lobes deeper than wide 17
16. Fore wings without humeral spots; aedeagal hamulus with two long, acuminate upturned points (Fig. 23); ventral parameres unbranched, with closely-set barbs along mesal edge ..... *P. bichai*
—Fore wings with both humeral spots; aedeagal hamulus broadly U-shaped, the two points acute or narrowly rounded; each ventral paramere with two long, slender branches; barbs on dorsal branch and base of ventral branch widely separated ..... *P. bifida*
17. Wings with two humeral spots, the second rarely faint 18
—Wings with only one (first) humeral spot, or none 21
18. Ventral parameres of male two-branched; basal plate of female genital plates crescent-shaped, covered ventrally by thick, sclerotized cuticular folds except along mid-line 19
—Ventral parameres with tufts of barbs but no branches; basal plate not distinctly separate from apical plate; no sclerotized folds of cuticle below genital plates 20
19. Ventral or lateral, shorter branch of each ventral paramere terminating in tuft of long barbs (or two tufts slightly separated); anterior apodemes of female genital plates (i.e., part before basal plate) about 35% of length of entire structure ..... *P. anomala*
—Ventral branch of ventral paramere with numerous short barbs, but without terminal tuft(s) of barbs; apodemes of female genital plates short, less than one-fourth (17-23%) of length of entire structure ..... *P. speciosa*
20. Ventral parameres short, curved, not extending between dististyles, with two tufts of short barbs on apical enlargement; apical genital plate of female with broad posterior projections ..... *P. braueri*
—Ventral parameres long, extending slightly between dististyles, nearly straight, with basal tuft of barbs from semimembranous expansion on mesal side of paramere and two divergent tufts of long barbs at and near apex; apical genital plate of female with slender posterior projections ..... *P. isolata*
21. Inner basal cups largely on ventral (posterior) surface of dististyles (Figs. 30, 31); ventral margin of cup usually irregularly serrate and set laterad, concave inner surface of cup facing ventrad or nearly so; genital plates of female without apodemes extending anteriorly from basal plate (Figs. 38, 40) (*banksiana* group) 22
—Inner basal cups of dististyles facing toward region between basistyles, toward aedeagus; genital plates of female with conspicuous anterior apodemes 24
22. Ventral parameres without barbs, broad at base (as wide as hypovalves), attenuate toward slender apex, extending almost to ends of dististyles (Fig. 30); basal cup of dististyle as wide as long; genital plates of female (Carpenter, 1931, fig. 53) narrowly rounded anteriorly ..... *P. banksiana*
—Ventral parameres with barbs along most of mesal edge, not broad at base; basal cup of dististyle oblong, narrower than long; anterior end of genital plates of female wide, scarcely rounded 23
23. Ventral parameres strongly bowed, tips broadly overlapping (Fig. 31); basal cup of dististyle not divided by a carina; genital plates of female almost truncate anteriorly (Fig. 38) ..... *P. gracilis*
—Ventral parameres slightly curved, not enough to overlap apically; basal cup of dististyle divided by a diagonal carina; genital plates of female broadly bilobed anteriorly (Fig. 40) ..... *P. palustris*
24. No complete bands or large spots on wings; most cross-veins conspicuously bordered with dark pigmentation, borders wider than cross-veins ..... *P. vernalis*
—Both apical and pterostigmal bands usually complete (but pale spots may be enclosed by apical band); cross-veins not conspicuously bordered 25

25. First humeral spot absent (rarely present but faint); pterostigmal band complete, not conspicuously narrowed behind M_{1+2}; cross-veins not bordered; basal cup of dististyles without darkened angle or tooth on dorso-mesal margin; apical plate of female genital plates with slender posterior lobes about twice as long as width at base ..... *P. insolens*

—First humeral spot present; pterostigmal band narrowed behind M_{1+2} or rarely interrupted; some cross-veins narrowly bordered; basal cups of dististyles with darkened angular tooth on dorso-mesal margin; apical plate of female genital plates with posterior lobes only slightly longer than width at base, or shorter (*rufescens* group) 26

26. Ventral parameres short, free (apical) portion of each extending only slightly beyond adjacent basistylar flange, apical barbs not reaching ends of basistyles (Figs. 49, 54, 65) 27

—Ventral parameres longer, free portion of each usually extending beyond ends of basistyles, apical barbs often extending into cups of dististyles (Figs. 42, 72, 81, 86) 29

27. Ventral parameres with barbs along mesal side only (Fig. 49); laterotergites of female ninth segment conspicuous, evenly rounded posteriorly ..... *P. scopulifera*

—Ventral parameres with some barbs on outer subapical edge; laterotergites absent or concealed by subgenital plate 28

28. Sclerotized band in free portion of ventral paramere extending to or among apical barbs (Fig. 54, 55); usually no thick, black setae on ventro-mesal apex of basistyle (rarely 1 or 2); female without laterotergites on ninth segment of abdomen ..... *P. ferruginea*

—Sclerotized band not reaching end of free portion of ventral paramere (Fig. 66); 2-4 thick, black setae on ventro-mesal apex of each basistyle; female with small laterotergites usually concealed by upturned edges of subgenital plate ..... *P. confinis*

29. Barbs of ventral parameres short, slender, on dorsal or mesal surface of paramere (Figs. 103, 108), numerous and not clearly in rows 30

—Barbs on ventral parameres long, readily visible in ventral aspect, on mesal edge only or on both sides but fewer on outer edge than along mesal edge 32

30. Ventral parameres bowed laterad, barbs primarily on mesal surface (Fig. 103); basal plate of female genital plates conspicuously wider than apical plate; pale (thin) areas in basal plate at either side of axial portion (Figs. 105, 106); laterotergites present (Fig. 104) ..... *P. planicola*

—Ventral parameres bowed ventrad, barbs primarily on dorsal surface (Fig. 108); basal plate of female genital plates only slightly wider than apical (distal) plate (Fig. 110); laterotergites absent 31

31. Three or four thick, black setae on ventro-mesal apex of each basistyle, in male; ventral parameres protruding conspicuously from genital bulb; axial portion of genital plate of female extending beyond posteromedial margin of distal plate ..... *P. ensigera*

—No thick, black setae on ventro-mesal apex of basistyle; ventral parameres not protruding or scarcely protruding from genital bulb; axial portion of genital plate of female not extending to posteromedial margin of distal plate (Fig. 110) ..... *P. robusta*

32. Ventral parameres wide, flattened, bowed laterad, with long barbs along mesal edge only (Fig. 42); females with moderately sclerotized laterotergites having smooth outer surface (may be folded in dried specimens) ..... *P. hispida*

—Ventral parameres slender, straight or broadly sinuous, or short, thick and bowed ventrad, with few subapical barbs on outer (lateral) edge, greater number along mesal edge; laterotergites absent or small and usually concealed in dried specimens 33

33. Free portion of ventral parameres short, thick, about half distance from basistyle to mid-line (Fig. 72), bowed ventrad, with apical barbs often extending into cups of dististyles; laterotergites of female small, usually concealed by upturned edges of subgenital plate; 7 or 8 setae at each side on infolded dorsal edge of subgenital plate directed mesad ..... *P. pachymera*

—Free portion of ventral parameres long, slender, set near mesal surface of basistyle, with sharp, sclerotized apex extending among apical barbs or beyond (Figs. 82, 87); laterotergites small and apically rounded (Fig. 95) or absent but with moderately sclerotized cuticular folds beneath ninth tergum turned inward around base of genital plates; no mesally directed setae on upper edges of subgenital plate 34

34. Ventral paramere without barbs on apical 30 per cent of free portion; barbs long, some 30 per cent as long as free portion of paramere (Fig. 102); laterotergites of female small, rounded apically (Fig. 95) ..... *P. venosa*

—Ventral paramere with barbs extending to or nearly to tip; barbs shorter, longest ones less than 25 per cent of length of free portion of paramere (Figs. 81, 86); laterotergites not noticeably developed on ninth abdominal segmentof female 35

35. Four thick, black setae on ventro-mesal apex of each basityle (Fig. 86); known range in Arkansas ..... *P. rupeculana*

—Usually no thick, black setae on basistyle (rarely 1 or 2) (Fig. 81); known range in Georgia ..... *P. acuminata*

LITERATURE CITED

Banks, N. 1918. New neuropteroid insects. Bull. Mus. Compar. Zool., Harvard Coll. 62: 1-22.

Bicha, W. 1983. A new species of scorpionfly (Mecoptera: Panorpidae) from North Carolina. Proc. Entomol. Soc. Washington 85: 152-155.

Boese, Ann E. 1973. Descriptions of larvae and key to fourth instars of North American *Panorpa* (Mecoptera: Panorpidae). Univ. Kansas Sci. Bull. 50: 163-186.

Byers, G. W. 1954. Notes on North American Mecoptera. Ann. Entomol. Soc. America 47: 484-510.

———. 1962a. Descriptions and distributional records of American Mecoptera. II. J. Kansas Entomol. Soc. 35: 299-307.

———. 1962b. Type specimens of nearctic Mecoptera in European museums, including descriptions of new species. Ann. Entomol. Soc. America 55: 466-476.

———. 1963. The life history of *Panorpa nuptialis* (Mecoptera: Panorpidae). Ann. Entomol. Soc. America 56: 142-149.

———. 1973a. Descriptions and distributional records of American Mecoptera. III. J. Kansas Entomol. Soc. 46: 362-375.

———. 1973b. Zoogeography of the Meropeidae (Mecoptera). J. Kansas Entomol. Soc. 46: 511-516.

Caron, D. M. 1967. Habitat and distribution of Mecoptera in east Tennessee. J. Tennessee Acad. Sci. 42: 73-77.

Carpenter, F. M. 1931. Revision of the nearctic Mecoptera. Bull. Mus. Compar. Zool., Harvard Univ. 72: 205-277, pls. 1-8.

———. 1935. New nearctic Mecoptera, with notes on other species. Psyche 42: 105-122.

———. 1939. Records and notes of nearctic Mecoptera and Raphidiodea. Bull. Brooklyn Entomol. Soc. 34: 162-166.

Cole, A. C. and D. S. Gillespie. 1950. Mecoptera records from Tennessee. J. Tennessee Acad. Sci. 25: 84-85.

Esben-Petersen, P. 1921. Mecoptera. Collections Zoologiques du Baron Edm. de Selys Longchamps, fasc. 5 (2): 1-172, 188 figs., pls. 1-2.

Ferris, G. F. and B. E. Rees. 1939. The morphology of *Panorpa nuptialis* Gerstaecker (Mecoptera: Panorpidae). Microentomology 4: 79-108, 51 figs.

Gurney, A. B. 1937. A new species of *Panorpa* from Utah, with notes on other nearctic species (Mecoptera). Proc. Entomol. Soc. Washington 39: 222-227.

———. 1938. Synonymy in the genus *Panorpa* (Mecoptera). Proc. Entomol. Soc. Washington 40: 52.

International Commission on Zoological Nomenclature. 1985. International Code of Zoological Nomenclature. Third edition. xx + 338 pp.

Mampe, C. D. and H. H. Neunzig. 1965. Larval descriptions of two species of *Panorpa* (Mecoptera: Panorpidae), with notes on their biology. Ann. Entomol. Soc. America 58: 843-849.

Navás, L. 1913. Neuroptera asiatica. I series. Revue Russe d'Entomol. 13: 271-284.

Penny, N. D. and G. W. Byers. 1979. A check-list of the Mecoptera of the world. Acta Amazonica 9: 365-388.

Webb, D. W. 1974. New species of *Panorpa* (Mecoptera: Panorpidae). Entomol. News 85: 171-173.

THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. 55, No. 3, pp. 97–122 August 30, 1993

NOT
UNDER
OCT 26 1993
HARVARD
UNIVERSITY

Revision of the Bee Genus *Braunsapis* in the Australian Region (Hymenoptera: Xylocopinae: Allodapini)[1]

Stephen G. Reyes

TABLE OF CONTENTS

Introduction 98
Materials and Methods 98
Characters 98
Key to Females of Australian *Braunsapis* 100
Key to Males of Australian *Braunsapis* 101
The *diminuta* Species Group 102
B. diminuta (Cockerell), 102; *B. plebeia* (Cockerell), 103; *B. clarissima* (Cockerell), 104; *B. plumosa*, n.sp., 105; *B. diminutoides* n.sp., 105; *B. anthracina*, n. sp., 106
The *verticalis* Species Group 106
B. verticalis, n. sp., 106
The *simillima* Species Group 106
B. simillima (Smith), 106; *B. boharti* (Krombein), n. status, 108; *B. protuberans*, n. sp., 108; *B. unicolor* (Smith), 109; *B. nitida* (Smith), 111; *B. biroi* (Friese), 111
The *associata* Species Group 112
B. associata (Michener), 112; *B. praesumptiosa* (Michener), 112; *B. eximia*, n. sp., 113; *B. falcata*, n. sp., 113; *B. platyura*, n. sp., 113; *B. hirsuta*, n. sp., 114
The *minor* Species Group 114
B. occidentalis (Michener and Syed), 114; *B. minor* (Michener and Syed), 114; *B. dolichocephala*, n. sp., 114; *B. hyalina*, n. sp., 115
Acknowledgments 115
Literature Cited 115

ABSTRACT

The genus *Braunsapis* from the Australian region is revised; twenty-three species are treated. Eleven species are described as new, namely: *B. plumosa*, *B. diminutoides*, *B. anthracina*, *B. verticalis*, *B. protuberans*, *B. eximia*, *B. falcata*, *B. platyura*, *B. hirsuta*, *B. dolichocephala*, and *B. hyalina*. *Allodapula perkinsiella* Michener is synonymized under *B. clarissima* (Cockerell). *Allodapula mindanaonis boharti* Krombein is elevated to specific level as *B. boharti* (Krombein). Important characters used in discriminating the Australian species are discussed. Keys and illustrations are provided.

[1] Contribution Number 3104 from the Department of Entomology, University of Kansas, Lawrence, Kansas 66045

INTRODUCTION

Braunsapis Michener (1969) is a genus of the tribe Allodapini, of the apoid subfamily Xylocopinae. *Braunsapis* and another genus of Xylocopinae, *Ceratina* (Fig. 1), which also occurs in Australia, are sometimes easily confused but the former differs from the latter in having only two submarginal cells (Figs. 3, 4). In Australia, two other allodapine genera also occur: *Exoneurella* and *Exoneura*. These are endemic to Australia and can be readily distinguished from *Braunsapis* by lacking the second recurrent vein (Fig. 2). While *Braunsapis* is primarily tropical and subtropical, the other genera are most common in the temperate parts of Australia. Distinguishing features of these taxa are explained by Michener (1965). Michener and Syed (1962) studied the taxonomy of the Australian *Braunsapis*. Most of the important morphological features now used to distinguish the different species were already mentioned in this earlier study and are explained in detail in the section on Characters below.

For the purposes of the present work, the Australian Region is taken to include not only Australia but also Solomon Islands, New Guinea and neighboring islands, i.e., the area covered in the account of bees of the Australian and South Pacific region (Michener, 1965).

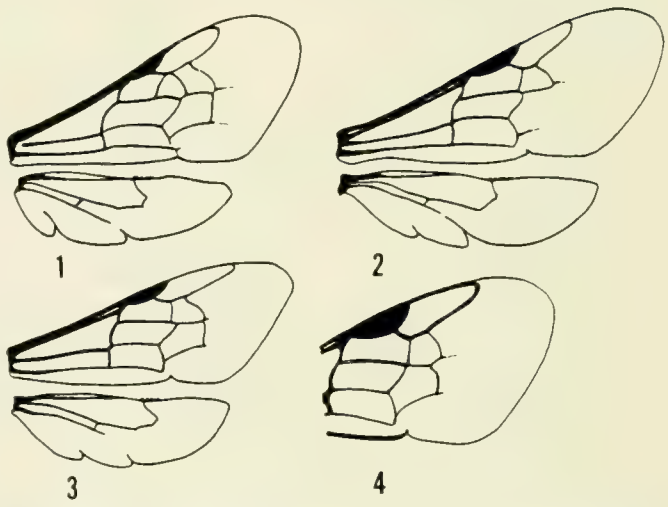
Thirteen trivial names have been proposed for species in the genus *Braunsapis* in Australia (mostly under the generic names *Allodape* and *Allodapula*). Michener (1965) also noted that certain other species described earlier under *Allodape* were misplaced. Thus *A. picta* Smith is in fact a *Euryglossa* (Family Colletidae) (as is also *A. grisea* Alfken) and *A. bribiensis* Cockerell belongs to the genus *Ceratina* in the Xylocopine tribe Ceratinini. The Australian species of *Braunsapis* although previously treated under the names *Allodape* and *Allodapula*, as was the case also for those of the Oriental region (Michener, 1961, 1962, 1965, 1966; Michener and Syed, 1962), were transferred as a group to *Braunsapis* by Michener (1969).

The biology and behavior of species of *Braunsapis* have been dealt with in numerous papers, such as: Michener (1961, 1962, 1966, 1968, 1970, 1971, 1974, 1990), Maeta *et al.* (1984, 1985, 1992), and Sakagami (1960). For Australia, see Michener (1961, 1962, 1965) and Michener and Syed (1962).

MATERIALS AND METHODS

The methods used in describing species follow the same protocol as in the earlier paper on Oriental *Braunsapis* (Reyes, 1991). In the descriptions, the characters are numbered to facilitate comparison among species. When numbers are omitted, the relevant characters are described for the first species of the species group. An asterisk instead of a number indicates a unique character. Abbreviations used in the descriptions and keys are HW (head width), HL (head length), T (metasomal tergum or terga) and S (metasomal sternum or sterna).

The acronyms below are used to indicate where specimens are deposited. For material studied I express my gratitude to the following individuals and museums:



Figs. 1-4. Wing of female. **Fig. 1.** *Ceratina australiensis* (Perkins). **Fig. 2.** *Exoneurella lawsoni* (Ravment). **Fig. 3.** *Braunsapis simillima* (Smith). **Fig. 4.** *B. biroi* (Friese).

AEI – American Entomological Institute, Gainesville, Florida (H.K. Townes).
AMNH – American Museum of Natural History, New York (M. Favreau).
ANIC – Australian National Insect Collection, Canberra, A.C.T. (J.C. Cardale).
Bishop – Bernice P. Bishop Museum, Honolulu, Hawaii (G. M. Nishida).
BMNH – The Natural History Museum, London (G.R. Else).
Budapest – Termèszettudomànyi Muzeum, Budapest, Hungary (P. Jenó).
CAS – California Academy of Sciences, San Francisco, California (N. Penny).
CU – Cornell University, Ithaca, New York (G.C. Eickwort).
LNHM – Natural History Museum of Los Angeles County, California (R. Snelling).
MCZ – Museum of Comparative Zoology, Cambridge, Massachusetts (J.M.Carpenter).
NMNH – National Museum of Natural History, Smithsonian Institution, Washington, D.C. (R.J. McGinley).
NMV – National Museum of Victoria, Melbourne (K. Walker).
QM – Queensland Museum, Brisbane (E.C. Dahms).
SAM – South Australian Museum, Adelaide.
SMUK – Snow Entomological Museum, University of Kansas, Lawrence, Kansas (C.D. Michener).
UQIC – University of Queensland, St. Lucia, Brisbane (E.M. Exley).
WAM – Western Australian Museum, Perth (T.F. Houston).

CHARACTERS

Adult characters are quite conservative in *Braunsapis* while the larvae seem to provide more characters to discriminate one species from another (Michener, 1977); Michener and Syed, 1962). Moreover, some characters, i.e., tegular color, hairs on T4-6, the carina defining the basitibial plate posteriorly or the clypeal markings, are quite variable in some species and conservative in others. Therefore, comments are

given on the different characters used in this study as was done for the Oriental species (Reyes, 1991).

a) Body length. Rough approximation of body length; specimens are measured in lateral view.

b) Color of labrum and mandible. Yellowish markings are quite variable in *B. plebeia, simillima* and *unicolor* where the mandibles may be black, partly or entirely yellow and the labrum partly or entirely yellow. In other species, this coloration is less variable.

c) Clypeal mark. In the males, the clypeus is largely yellow. The following note largely concerns the females. As in the Oriental species, this character is informative when used in combination with other characters such as head width and type and color of hairs on T4-6. The clypeus is either mostly yellow as in *B. plumosa* and *occidentalis* (Figs. 56, 82) or the lower half of clypeus is partly black, the yellow mark covering at least half the area as in *B. diminuta* , *plebeia* and *diminutoides* (Figs. 48, 51, 57) or the lower half of clypeus is mostly black, the yellow mark barely reaching the apex as in *B. boharti, unicolor* and *biroi* (Figs. 66, 70, 74).

d) Paraocular mark. Paraocular marks are yellow marks found between the lateral margin of the clypeus and the inner eye orbit. Females with broad clypeal markings sometimes have spots or marks on paraocular area as in the cases of *B. clarissima, diminuta, simillima,* and *biroi.* Males have the paraocular marks extensive to reduced in some species (Figs. 50, 53, 55) while they are absent in others (Figs. 49, 52).

e) Color of pronotal lobe. Yellow except in *B. anthracina* and *minor.*

f) Color of tegula and axillary sclerites. *B. nitida* and *unicolor* show variability in tegular color as shown (Fig. 5) for Queensland and Northern Territory populations. Transparent tegulae are prevalent in Northern Territory in both species and occur in more than 50% of the Queensland population of *B. nitida. B. unicolor,* on the other hand, has the tegulae mainly translucent fuscous or dark in Queensland.

g) Head width. Head width is the greatest distance between the outer surfaces of the compound eyes viewed frontally. This character is important in separating closely related species like *B. nitida* and *unicolor* and the four species of the *diminuta* group, namely: *B. diminuta, plebeia, diminutoides* and *clarissima.* The histogram of the head widths of *B. nitida* and *unicolor* (Fig. 6) showed a bimodal distribution and the difference of the means between the two species is very highly significant. From the same histogram, one might conclude that the head width of *B. nitida* should be between 1.16 – 1.43 mm. The upper limit , however, was set at 1.53 mm because other size-correlated characters (i.e., scape length, carina of the basitibial plate) differ somewhere around this point.

h) Head width/head length ratio. The head length is the greatest distance between the vertex and the apex of clypeus. This character is especially useful in separating the females of the *minor* species group, where the head is longer than broad or as long as broad. In the other species groups, the heads of the females are broader than long. All males have heads broader than long.

i) Malar space. This character refers to the length of the malar area; it is the minimum distance between the lower end of the compound eye and the base of the mandible. It is shorter than the width of the scape except in the three species of the *minor* group: *dolichocephala, minor* and *occidentalis.*

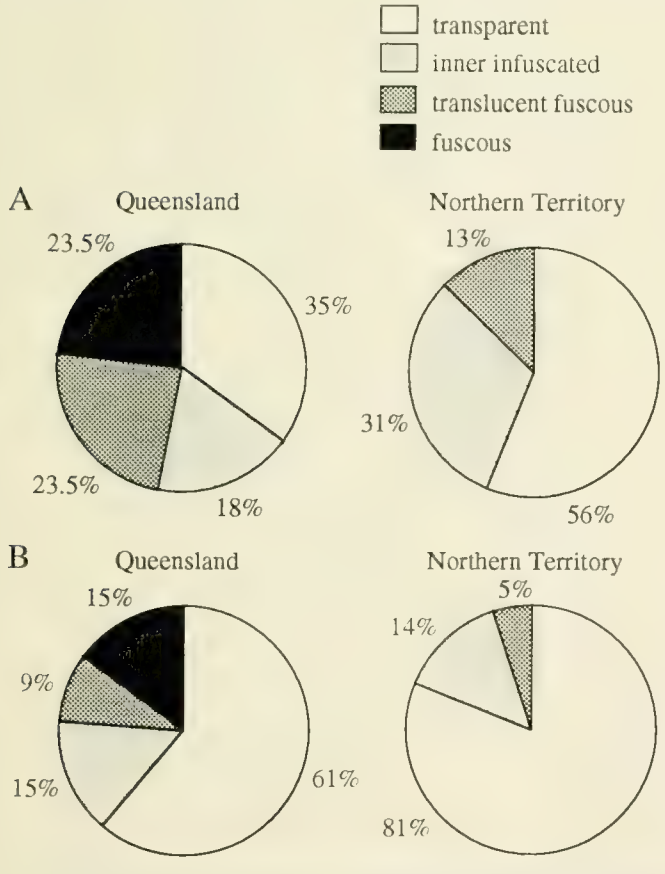


Fig. 5. Distribution of tegular color in (A) *B. nitida* (n = 34, 94) and (B) *B. unicolor* (n = 96, 21) from Queensland and Northern Territory, respectively.

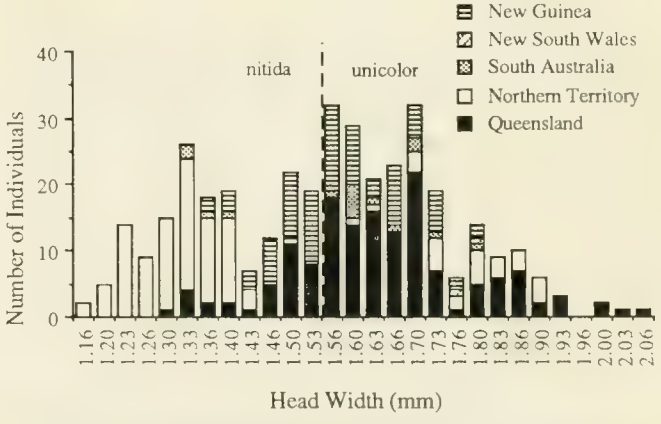


Fig. 6. Histogram of head widths of *B. nitida* (n = 168) and *B. unicolor* (n = 208).

j) Middle of epistomal suture. This area is sometimes slightly elevated in lateral view. The center of the elevated area lies on the upper limit of clypeus and includes the surrounding area both above and below the epistomal suture.

k) Length of scape. As with the Oriental species, specimens with the head width over 1.53 mm have the scape reaching the front ocellus or sometimes the posterior ocelli, especially in the largest individuals. In smaller specimens with the head width 1.53 mm or less, the scape does not reach the front ocellus. Plotting the head width versus the length of the scape shows no sign of allometry.

l) Basitibial plate of female. This plate is not well developed in Allodapini but sometimes is defined posteriorly by a carina or a conical protuberance; otherwise it is indistinct. Larger individuals usually have a distinctly raised or acute carina or conical protuberance while smaller ones have the carina weak, indistinct or absent. Some species such as *B. praesumptiosa* and *nitida* show variability in this character but the majority of the individuals in both exhibit the same trend as with the other species (Table 1).

Table 1. Variation in the form of the carina of the basitibial plate of females in the species of *Braunsapis*. Head width measurements are in millimeters. Ind. = indistinct, Wk. = weak, Rsd. = raised, N = total number of specimens examined.

Species	Head width (mm)	Mean ± Std. dev.	Percentage			N
			Ind.	Wk.	Rsd.	
protuberans	1.90 – 2.37	2.11 ± .11			100	101
verticalis	1.80 – 2.20	2.02 ± .09		9	91	43
praesumptiosa	1.63 – 2.23	2.00 ± .14	19	12	69	32
plebeia	1.57 – 1.93	1.73 ± .12		13	87	105
diminuta	1.23 – 1.53	1.44 ± .06	6	60	34	108
falcata	1.39 – 1.56	1.39 ± .09	7	93		30
nitida	1.16 – 1.53	1.37 ± .11	11	83		125
eximia	1.20 – 1.43	1.33 ± .08	100			11
hyalina	1.16 – 1.53	1.21 ± .06	88	12		91

m) Hairs on T4-6. As for the Oriental species, descriptions are of the middorsal hairs. The longer hairs (hair length usually less than the width of scape) may be plumose as in *B. plebeia* or *B. diminuta* (Fig. 95), spiculate as in *B. verticalis* (Fig. 96), or blunt or simple as in *B. clarissima* (Fig. 97). Hair color is useful, especially for field collected females, but may not be useful for young females or callows collected or reared from the nests. Such individuals have pale hairs, even in species whose hairs are black in mature adults.

n) Male trochanter. Either notched midventrally and lobed apically or simple. Femora of the males are not modified and notched as in some African and Oriental species (Michener, 1975; Reyes, 1991).

o) Male genitalia. The genitalia are quite important in discriminating the species of *Braunsapis* though some parts are variable among individuals of the same species, e.g., the number of teeth or peg-like processes on the ventro-apical plate. As in the Oriental species (Reyes, 1991), the roof of the genital chamber is wrinkled in all the specimens examined; no Australian species were found having a smooth surface as do some African species (Michener, 1975).

Some terminology was introduced and explained earlier on the different forms of the penis valve (Reyes, 1991; c.f. figs. 26, 27). The mid-lateral flange of the penis valve (MLF), the anterior projection (AP) and the posterior projection (PP) are shown in Fig. 13. The dorso-lateral gap (DLG) could not be clearly shown when the penis valve is drawn in dorso-apical position as done here, but it is the space between the base of the mid-lateral flange and the apex of the posterior projection of the penis valve. The width of the gap is useful in differentiating some species and appears to be consistent within species. A broad mid-lateral flange of the penis valve is found in some species as in Figs. 13, 25 and 34 or may be entirely absent as in *B. clarissima* (Fig. 16). Similarly as in the Oriental species, the ventro-apical plates (VAP) can be symmetrical or asymmetrical; that is, both the right and left plates may have the same number of peg-like processes or one plate may have fewer peg-like processes than the other. The number of genitalic dissections is indicated in the descriptions, e.g. (n = 2).

As indicated above, some characters vary with general size, both between and within species, so that the larger individuals in general have a scape that reaches higher on the head and a stronger carina of the basitibial plate. When such characters are ignored as correlates of general size, which is best represented by head width in the above list of characters, certain species differ almost only in size. Such characters are included, however, in the key and descriptions, not only because they would help a user in making identifications but because they sometimes sharpen the distinction between species (see head width above). For studies of phylogeny or degree of difference among species, such characters should doubtless be omitted because of the correlation with head width.

KEY TO FEMALES OF *BRAUNSAPIS* OF THE AUSTRALIAN REGION

1. T6 with dorsal surface concave, scoop-shaped, lateral margins produced to elevated shoulders; apex not more densely hairy than rest of tergum, rounded (Figs. 92, 93) 2
—T6 with dorsal surface convex, lateral margins not produced, extreme apex often hidden or obscured by hair, minutely notched or emarginate (Fig. 94) 7
2. Hairs on T4-6 transparent to light fuscous 3
—Hairs on T4-6 fuscous to black 5
3. T6 with tip and lateral margin only slightly curved as in Fig. 93. (Hairs on T4-5 simple, usually more than twice as long as width of scape.) ..... *platyura*
—T6 with tip and lateral margin strongly curved as in Fig. 92 4
4. Longer hairs on T4-5 blunt to spiculate, less than twice as long as width of scape; basitibial plate with carina weak, sometimes indistinct ..... *falcata*

—Longer hairs on T4-5 simple, about twice as long as width of scape; basitibial plate with carina raised ..... *hirsuta*

5. T6 with tip and lateral margin slightly curved (Fig. 93) ..... *praesumptiosa*

—T6 with tip and lateral margin strongly curved as in Fig. 92 6

6. Head width 1.66 - 1.90 mm; head about 1.1 times broader than long; scape reaching front ocellus; basitibial plate with carina conically produced ..... *associata*

—Head width 1.20 - 1.43 mm; head about 1.04 times broader than long; scape not reaching front ocellus; basitibial plate with carina weak or indistinct ..... *eximia*

7. Vertex sharply declivous posteriorly, almost carinate, densely and coarsely punctate behind posterior ocelli (Fig. 90). (Facial mark broad; epistomal suture seen in profile raised; tegula transparent; axillary sclerite yellow; basitibial plate bordered by strong carina apically; hairs on T4-6 curved, spiculate, slightly longer than width of scape) ..... *verticalis*

—Vertex gradually angular, not coarsely punctate behind posterior ocelli, as in Fig. 91 8

8. Body pubescence, including scopa, fulvous. (Clypeal mark broad, paraocular area often with yellow mark above tentorial pit; tegula transparent, translucently fuscous mesally; axillary sclerite yellow; middle of epistomal suture seen in profile raised; basitibial plate bordered apically by weak carina; metasomal hairs suberect, curved, simple, thick, some blunt, shorter than width of scape) ..... *boharti*

—Body pubescence whitish 9

9. Head as long as or longer than broad 10

—Head broader than long. (In some cases an ocular micrometer is important to make this distinction) 13

10. Malar space about twice as long as width of scape. (Clypeal mark broad; middle of epistomal suture seen in profile raised; tegula transparent; axillary sclerite yellow; basitibial plate bordered posteriorly by weak carina; hairs on T4-6 slanting, curved, transparent, plumed at tips) ..... *dolichocephala*

—Malar space less than twice width of scape 11

11. Malar space slightly longer than width of scape. (Pronotal lobe yellow; hairs on T4-6 suberect, curved, transparent, plumed; clypeal mark broad; middle of epistomal suture seen in profile raised; tegula transparent; axillary sclerites yellow; basitibial plate bordered posteriorly by weak carina) ..... *occidentalis*

—Malar space shorter than width of scape 12

12. Pronotal lobe black and hairs on T4-6 black ..... *minor*

—Pronotal lobe yellow and hairs on T4-6 transparent ..... *hyalina*

13. Pronotal lobe black; clypeal mark usually absent, if present, represented by small transverse mark at base. (Middle of epistomal suture seen in profile raised; tegula and axillary sclerite dark; basitibial plate bordered posteriorly by weak carina; hairs on T4-6 suberect, curved, transparent simple, slightly longer than width of scape) ..... *anthracina*

—Pronotal lobe yellow; clypeus with yellowish markings not limited to transverse mark at upper margin.... 14

14. Hairs on T4-6 light fuscous or transparent 15

—Hairs on T4-6 fuscous or black 19

15. Prostrate hairs on T4-6 strongly plumose ..... *plumosa*

—Subprostrate or prostrate hairs on T4-6 simple or spiculate 16

16. Longer hairs on T4-6 simple, about or over twice as long as width of scape as in Fig. 97 17

—Longer hairs on T4-6 plumose or spiculate as in Figs. 95, 96, less than twice as long as width of scape 18

17. Head width 1.40 - 1.53 mm; scape not reaching front ocellus ..... *diminutoides*

—Head width 1.57 - 1.90 mm; scape reaching front ocellus ..... *clarissima*

18. Head width 1.23 - 1.53 mm; scape not reaching front ocellus ..... *diminuta*

—Head width 1.57 - 1.96 mm; scape reaching front ocellus ..... *plebeia*

19. Middle of epistomal suture seen in profile conically raised (Fig. 88) ..... *protuberans*

—Middle of epistomal suture seen in profile only slightly raised (Fig. 89) 20

20. Second recurrent vein about one-third length of second submarginal cell basad from second transverse cubital (Fig. 4) ..... *biroi*

—Second recurrent vein less than one-third length of second submarginal cell basad from second transverse cubital 21

21. Clypeal mark narrow, strongly tapering towards apex as in Figs. 70, 71 22

—Clypeal mark broad, gradually tapering towards apex (Fig. 63) ..... *simillima*

22. Head width 1.16 - 1.53 mm; scape not reaching front ocellus ..... *nitida*
Head width 1.57 - 1.90 mm; scape reaching front ocellus ..... *unicolor*

KEY TO MALES OF *BRAUNSAPIS* OF THE AUSTRALIAN REGION

(Males are unknown or unrecognized for the following species: the *associata* species group, *occidentalis*, *minor*, *plumosa* and *biroi*).

1. Hind trochanter lobed apically and notched medially 2

—Hind trochanter not lobed or notched 7

2. Hairs on T4-6 transparent, simple ..... *hyalina*

—Hairs on T4-6 fuscous to black 3

3. Vertex sharply declivous posteriorly as in Fig. 90 ..... *verticalis*

—Vertex gradually declivous posteriorly as in Fig. 91 4

4. Middle of epistomal suture seen in profile conically raised as in Fig. 88 ..... *protuberans*

—Middle of epistomal suture seen in profile not strongly raised, as in Fig. 89 5

5. Scape usually yellow beneath; paraocular mark sometimes extensive, usually reaching the upper level of clypeal mark as in Fig. 65, but sometimes absent as in Fig. 64 ..... *simillima*
—Scape usually without yellowish markings, at most a yellowish spot beneath; paraocular mark absent or sometimes minute as in Figs. 71, 73 6
6. Head width 1.23 - 1.50 mm; scape not reaching front ocellus ..... *nitida*
—Head width 1.63 - 1.86 mm; scape reaching front ocellus ..... *unicolor*
7. Pronotal lobe and tarsi black ..... *anthracina*
—Pronotal lobe and tarsi yellow 8
8. Longer hairs on T4-6 long, simple, one and a half to two times as long as width of scape 9
—Longer hairs on T4-6 shorter, blunt to plumose or apparently simple, at most slightly longer than width of scape 10
9. Head width 1.27 - 1.53 mm; scape not reaching front ocellus ..... *diminutoides*
—Head width 1.57 - 1.76 mm; scape reaching front ocellus ..... *clarissima*
10. Head width 1.16–1.53 mm; scape not reaching front ocellus ..... *diminuta*
—Head width 1.57–1.93 mm; scape reaching front ocellus ..... *plebeia*

THE *DIMINUTA* SPECIES GROUP

The members of this group have the following characters: hairs on T4-6 transparent to light fuscous; head less broad than in the *simillima* species group; males with hind trochanter simple. The females of this group have broad clypeal marks gradually tapering towards the apex (Figs. 48, 51, 54, 56, 57), except for *B. anthracina*, which has a black clypeus.

Braunsapis diminuta (Cockerell)

Allodape diminuta Cockerell, 1915, p. 266. Types: female and 2 males, Yarrawin, New South Wales (NMNH).
Allodapula diminuta (Cockerell): Michener and Sved, 1962, p. 40; Michener, 1965, p. 233.

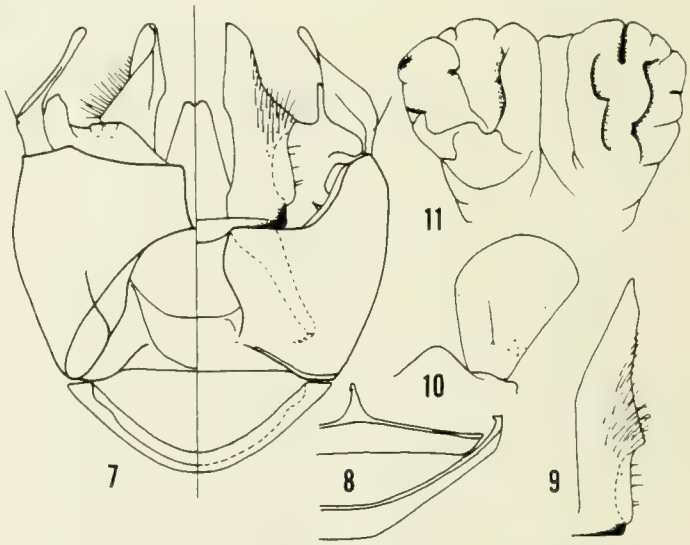
Lectotype: female, Yarrawin, New South Wales (NMNH), hereby designated (not a male as listed by Cardale, 1993).

Paralectotype: 2 males, same data as lectotype (NMNH). There were three specimens glued on a card with the type label on the pin. With permission from NMNH, the specimens were remounted and the female is here designated as the lectotype (since Cockerell's description is largely based on the female), the two males as paralectotypes. The specimens have been labelled accordingly.

Female. Face as in Fig. 48. (1) Length 4.00 - 6.00 mm. (2) Labrum and mandible black. (3) Lower half of clypeus partly black. (4) Paraocular mark absent. (5) Pronotal lobe yellow. (6) Tegula transparent, axillary sclerites yellow. (7) HW 1.23 - 1.53 mm. (8) HW/HL ratio 1.04 - 1.09. (9) Malar space shorter than width of scape. (10) Middle of epistomal suture slightly raised. (11) Scape not reaching front ocellus. (12) Basitibial plate with carina weak, sometimes raised, rarely indistinct. (13) Hairs on T4-6 transparent; longer hairs slanting, spiculate to plumose, as long as or slightly longer than width of scape; shorter hairs prostrate, spiculate to plumose (Fig. 95).

Male. Face as in Figs. 49-50. (14) Length 3.40 - 6.00 mm. (15) Labrum yellow, mandible fuscous. (16) Clypeus yellow. (17) Paraocular mark absent, reduced or extensive. (*) Scape sometimes with yellow mark on underside. (18) HW 1.10 - 1.53 mm. (19) HW/HL ratio 1.14 - 1.17. (20) Hind trochanter simple. (21) Hairs on T4-6 transparent; longer hairs suberect, simple to blunt, as long as or slightly longer than width of scape; shorter hairs prostrate to subprostrate, slightly spiculate. (22) Genitalia (n = 18) as in Figs. 7-11; gonostylus longer than broad, with one short seta (Fig. 10); ventro-apical plate of gonocoxite either symmetrical or asymmetrical, right plate with 1-4 peg-like processes, left plate with 1-5 peg-like processes; penis valve with mid-lateral flange narrow, posterior margin rounded, dorso-lateral gap wider than mid-lateral flange (Fig. 9); S7 and S8 as in Fig. 8; roof of genital chamber wrinkled (Fig. 11).

Specimens Examined. Types as listed. **Queensland**. 4 females, Prince of Wales Is., Torres Strait, 27-30.v.69, Neboiss (NMV); 1 female, 36 km. W of Mt. Carbine, 31.x.78, E.M. Exley and K. Walker (UQIC); 1 female, Hamilton Hotel, 28.x.72, E.F. Riek (ANIC); 3 females, 28 km. S of Mt. Isa, 4.xii.74, R.I. Storey (UQIC); 1 female, Mt. Boppy, 29.xi.49, E.F. Riek (ANIC); 3 females, 16° 24'S 144° 47'E, Kelly St. George River, 14 km. W of Mt. Desailly, 26.iv.86, I.D. Naumann (ANIC); 27 females, 3 males, 13 mi. W of Georgetown, 260 m., 4.x.62, E.S. Ross and D. Cavagnaro (CAS); female, Rockhamptom, 12.viii.58, C.D. Michener (SMUK); 1 female, 6 mi. W of Chinchilla, 14.iv.69, T.F. Houston (UQIC); 1 female, Macleod River, 15 km. W of Mt. Carbine, 22-23.vi.75, S.R. Monteith (ANIC); 1 female, 7 mi. W of Charleville, 1.xi.71, E.M. Exley (UQIC); 1 male, Cunnamulla, N. Geary (MCZ); 1 female, Proserpine, 9.viii.66, J.C. Cardale (UQIC); 10 females, 3 males, 31 km. E of Camooweal, 12.xii.88, R.R. Snelling and J. Grey (LNHM). **Northern Territory**. 2 females, Macdonald Dwns, 400 m., 30.x.62, E.S. Ross and D. Cavagnaro (CAS); 1 female, 12° 28'S 132° 52'E, Jabaluka (=Jabiluka) Lagoon, 14 km. N of Mudginbarry HS., 14.xi.72, J.C. Cardale (ANIC); 1 female, 12° 25'S 132° 58'E, 1 km. N of Cahill Crossing (E Alligator River), 8-9.xi.72, J.C. Cardale (ANIC); 9 females, 7 males, 12° 17'S 133° 20'E, Cooper Creek, 11 km. S by W of Nimbuwah Rock, 3-4.vi.73, J.C. Cardale (ANIC); 1 female, 12° 17'S 133° 16'E, 14 km. SW of Nimbuwah Rock, 11.xi.72, J.C. Cardale (ANIC); 1 female, 12° 17'S 133° 16'E, Birraduk Creek, 4-5.vi.73, J.C. Cardale (ANIC); 2 females, 12° 20'S 133° 4'E, Oenpelli Hill, 11.xi.72, J.C. Cardale (ANIC); 4 females, 12° 47'S 132° 51'E, 19 km. NE by E of Mt. Cahill, 13-16.xi.73, J.C. Cardale (ANIC); 1 female, 12° 50'S 132° 51'E, 16 km. E by N of Mt. Cahill, 13.vi.73, J.C. Cardale (ANIC);



Figs. 7-11. Male genitalia of *B. diminuta*, Cunnamulla, Queensland. **Fig. 7.** Dorsal (right) and ventral (left) view of genitalia. **Fig. 8.** S7 and S8. **Fig. 9.** Penis valve, dorso-apical view. **Fig. 10.** Gonostylus, lateral view . **Fig. 11.** Roof of genital chamber.

1 female, 12° 52'S 132° 47'E, Nourlangie Creek, 8 km. E of Mt. Cahill, 17-18.xi.72, J.C. Cardale (ANIC); 1 female, 12° 52'S 132° 46'E, Nourlangie Creek, 6 km. E of Mt. Cahill, 18.xi.72, J.C. Cardale (ANIC); 1 female, 12° 48'S 132° 42'E, Nourlangie Creek, 8 km. N of Mt. Cahill, 19-20.xi.72, J.C. Cardale (ANIC); 2 females, Darwin, 8.i.64, J. Sedlacek (Bishop); 8 females, MacArthur River, 16° 27'S 136° 5'E, 48 km. SW by S of Borroloola, 29.x.75, J.C. Cardale (ANIC); 1 female, 16° 3'S 136° 19'E, 3 km. N by E of Borroloola, 31.x.75, J.C. Cardale (ANIC); 18 females, 4 males, 15° 58'S 136° 21'E, 12 km. NNE of Borroloola, 1.xi.75, J.C. Cardale (ANIC); 16 females, 16° 8'S 136° 6'E, 22 km. WSW of Borroloola, 2.xi.75, J.C. Cardale (ANIC); 2 females, 16° 19'S 136° 5'E, 36 km. SW of Borroloola, 4.xi.75, J.C. Cardale (ANIC); 3 females, Cattle Creek, 16° 32'S 136° 10'E, 54 km. S by W of Borroloola, 27.x.75, J.C. Cardale (ANIC); 2 females, Goose Lagoon, 16° 10'S 136° 15'E, 11 km. SW by S of Borroloola, 31.x.75, J.C. Cardale (ANIC); 22 females, 11° 1'S 136° 45'E, Rimbija Is., Wessel Islands, 20.i - 3-14.ii.77, E.D. Edwards and T.A. Weir (ANIC); 9 females, 19 km. N of Daly Waters, 16.xi.74, E.M. Exley and R.I. Storey (UQIC); 1 female, 25 mi. N of Katherine, 16.iii.79, E.M. Exley (UQIC); 1 female, 39 km. N of Katherine, 22.xi.74, E.M. Exley and R.I. Storey (UQIC); 1 female, Stuart H'way, 160 km. S of Katherine, 25.xi.72, D.H. Colless (ANIC); 1 female, 17 km. N of Pine Creek, 22.xi.74, E.M. Exley and R.I. Storey (UQIC); 1 female, 8 km. N of Mataranka, 19.xi.74, E.M. Exley and R.I. Storey (UQIC); 1 female, Elsey Cemetery, 19 km. S of Mataranka, 18.xi.74, E.M. Exley and R.I. Storey (UQIC); 1 female, Jabiru, 5-9.vi.84, I.D. Naumann (ANIC); 1 female, 23° 40'S 133° 52'E, 7 km. N of Alice Spring, 8.v.78, J.C. Cardale (ANIC). **Western Australia**. 1 female, Goose Hill Creek, SE of Wyndham, 10 m, 21.x.62, E.S. Ross and D. Cavagnaro (CAS); 11 females, 15° 2'S 126° 55'E, Drysdale River, 3-8.viii.75, I.F.B. Common and M.S. Upton (ANIC); 7 females, 14° 49'S 126° 49'E, Carson escarpment, 9-15.viii.75, I.F.B. Common and M.S. Upton (ANIC); 14 females, 14° 49'S 125° 44'E, Mining Camp, Mitchell Plateau, 13-19.v.83, I.D. Naumann and J.C. Cardale (ANIC); 5 females, 14° 40'S 125° 44'E, Surveyors Pool, 15.v.83, I.D. Naumann and J.C. Cardale (ANIC); 1 female, 15 mi. S of Kununurra, 7.ii.78, E.M. Exley (UQIC); 6 females, 15° 46'S 128° 38'E, 10 km. W by N of Kununurra, 8.v.83, I.D. Naumann and J.C. Cardale (ANIC); 3 females, 14° 34'S 125° 50'E, 1 km. W of Mt. Walsh Point, 10.v.83, I.D. Naumann and J.C. Cardale (ANIC); 1 female, 24° 55'S 128° 48'E, 28 km. W by S of Docker River, 17.xi.77, M.S. Upton (ANIC); 9 females, NW Coastal H'way, 48 km. N of Murchison River Crossing, 6.i.76, E.M. Exley and R.I. Storey (UQIC); 3 females, Broome, 14.xii.75, E.M. Exley and R.I. Storey (UQIC); 1 female, 1 male, Gascoyne Expt. Sta., Carnarvon, 3-7.x.69, H.E. Evans and R.W. Matthews (MCZ); 1 female, 7 km. S of Carnarvon, 2.i.76, E.M. Exley and R.I. Storey (UQIC); 1 female, 8 km. S of Carnarvon, 4.i.76, E.M. Exley and R.I. Storey (UQIC); 5 females, 13 km. S of Carnarvon, 4.i.76, E.M. Exley and R.I. Storey (UQIC); 4 females, 16 km. E of Carnarvon, 3.i.76, E.M. Exley and R.I. Storey (UQIC); 9 females, Port Smith, 27.xi.88, R.R. Snelling and J. Grey (LNHM). **New South Wales**. 1 female, Bourke, 15.xii.76, E.M. Exley and T. Low (UQIC).

Remarks. The females from Western Australia and Northern Territory usually have the hairs on T4-6 whitish, plumose, prostrate, shorter than the width of the scape. The prostrate plumose hairs gradually vary to subprostrate or suberect, the latter only plumose or spiculate at the tips. Some females from Northern Territory (7 specimens, Wessel Is., ANIC) have slender clypeal markings similar to those of *B. hyalina* (Fig. 86), but the head is clearly broader than long as in *B. diminuta*. Females from Western Australia have a relatively larger carina of the basitibial plate.

Braunsapis plebeia (Cockerell)

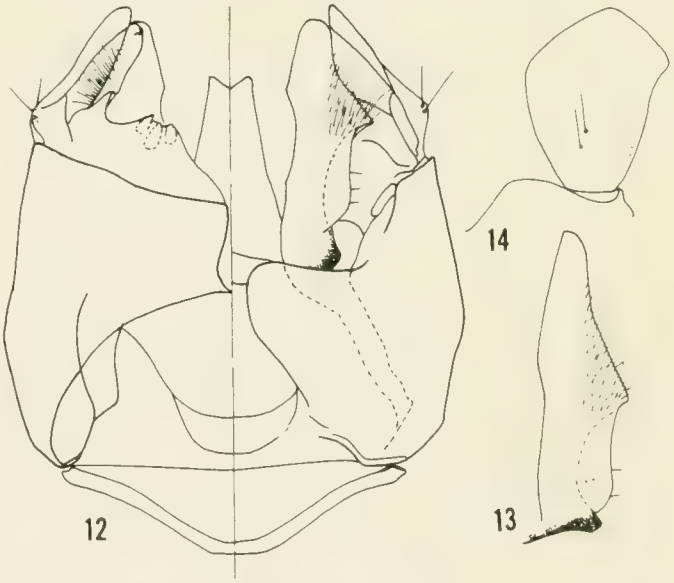
Allodape plebeia Cockerell, 1929a, p. 15. Type: male, Thursday Island, Queensland (NMNH). [Female cotype (=paratype) is *B. simillima* (Smith)].

Allodapula plebeia (Cockerell): Michener and Syed, 1962, pp. 34, 40-41; Michener, 1965, p. 233.

Female. Face as in Fig. 51. (1) Length 6.00 - 8.00 mm. (6) Tegula transparent to dark, axillary sclerites yellow. (7) HW 1.56 - 1.96 mm. (8) HW/HL ratio 1.06 - 1.10. (10) Middle of epistomal suture slightly raised. (11) Scape reaching front ocellus. (12) Basitibial plate with carina conically raised, sometimes weak. (13) Hairs on T4-6 transparent to light fuscous; longer hairs slanting, spiculate to plumose, about as long as width of scape; shorter hairs prostrate, spiculate to plumose.

Male. Face as in Figs. 52, 53. (14) Length 5.00 - 6.50 mm. (15) Labrum and mandible black or with variously developed yellowish marks. (16) Lower half of clypeus partly black (Fig. 52) or entirely yellow (Fig. 53). (18) HW 1.63 - 1.90 mm. (19) HW/HL ratio 1.14 - 1.18. (21) Hairs on T4-6 transparent to light fuscous; longer hairs suberect, slender, as long or slightly longer than width of scape; shorter hairs prostrate, spiculate. (22) Genitalia (n = 5) as in Figs. 12-14; gonostylus narrowed at apex, with 1-2 short setae (Fig. 14); ventro-apical plate of gonocoxite either symmetrical or asymmetrical, right plate with 2-3 peg-like processes, left plate with 2-4 peg-like processes; penis valve with mid-lateral flange broad, dorso-lateral gap wider than mid-lateral flange (Fig. 13).

Specimens examined. Type as listed. **New Guinea**. 4 females, 3 males, Port Moresby, Papua, 25.iv.59, C.D. Michener (SMUK); 16 males, same data except (Bishop); 1 female, Port Moresby, Papua, 19.v.66, E.J. Ford Jr. (Bishop); 1 female, 25 mi. radius of Port Moresby, Papua, iv.28, Pemberton (Bishop); 1 female, 18 males, Roku, Central Dist., Papua, 23.iv.59, C.D. Michener (Bishop). **Queensland**. 3 females, 13 mi. W of Georgetown, 260 m., 4.xi.62, E.S. Ross and D. Cavagnaro (CAS); 56 females, 4 males, Prince of Wales Is., 14.ii.39, R.G.Wind (CAS); 3 females, 1 male, same data except (SMUK); 1 female, 1 male, same data except (AMNH); 3 females, Prince of Wales Is., 27-30.v.69, Neboiss (ANIC); 1 female, Prince of Wales Is., vii.20, J.A. Kusche (Bishop); 2 males, Moa (Banks) Is., 5 km WSW of St. Paul, Torres Strait, 16.vii.77, S.R. Monteith and D. Cook (UQIC); 1 female, Iron Range, Cape York Peninsula, 1-9.vi.71, S.R. Monteith (ANIC); 4 females, 11° 40'S 142° 50'E, Capt. Billy Creek, Cape York Peninsula, 9-14.vii.75, S.R. Monteith (ANIC); 1 female, Cape York Peninsula, 16-17.iv.73, S.R. Monteith (ANIC); 1 female, Thursday Is., Cape York, ix.20, J.A. Kusche (Bishop); 3 females, 16° 24'S 144° 47'E, Kelly St. George River, 14 km. W of Mt. Desailly, 26.iv.81, I.D. Naumann (ANIC); 1 female, Morven, 31.x.71, E.M. Exley (UQIC); 1 female, Glenmorgan, 22.x.58, C.D. Michener (SMUK); 6 females, 2 males, 28-40 mi. S Palmer River, Cooktown H'way, 18.v.75, R.I. Storey (UQIC); 1 female, 15° 29'S 145° 16'E, Mt. Cook National Park, Cooktown, 11-12.x.80, J.C. Cardale (ANIC); 4 females, 1 male, 26 mi. W of Mt. Garnet, 26.v.75, R.I. Storey (UQIC); 1 female, 8 mi. S of Mt. Isa, 20.iii.73, E.M. Exley (UQIC); 1 female, 7 mi. W of Charleville, 1.xi.71, E.M. Exley (UQIC); 2 females, 15° 6'S 145° 14'E, 12-14 km. ESE of Mt. Webb, 3.x.80, J.C.



Figs. 12-14. Male genitalia of *B. plebeia*, Smith Point, Cobourg Peninsula, Northern Territory. **Fig. 12.** Dorsal (right) and ventral (left) view of genitalia. **Fig. 13.** Penis valve, dorso-apical view. **Fig. 14.** Gonostylus, lateral view.

Cardale (ANIC); 1 female, 15° 10'S 145° 7'E, 3.5 km. SW by S of Mt. Baird, 3-5.v.81, I.D. Naumann (ANIC); 1 female, 15° 3'S 145° 15'E, 4 km. SW of Casuarina Hill, 30.iv - 2.v.81, I.D. Naumann (ANIC); 1 female, 16° 7'S 144° 47'E, Palmer River, 5 km. S by W of Mt. Herman, 27.ix.80, J.C. Cardale (ANIC); 1 female, Cook H'way, N. Cairns, 18.viii.67 (SAM); 1 female, Watalgan Range, 40 mi. WNW of Bundaberg, 7.x.72, H. Frauca (ANIC); 2 females, Mackay, xii.99 (BMNH); 1 female, near Rosedale, 27.x.74, H. Frauca (ANIC); 1 female, Normanby River Crossing, 6.viii.67, T.F. Houston (SAM); 1 female, 12 km. W of Fairview via Laura, 26.vi.75, S.R. Monteith (ANIC); 1 female, Brisbane, 9.iv.11, H. Hacker (QM); 1 female, Cape Pallarenda, 11.viii.66, J.C. Cardale (UQIC); 1 female, Cunnamulla, 21.x.75, J.C. Cardale (ANIC); 9 females, 1 male, 31 km. E of Camooweal, 12.xii.88, R.R. Snelling and J. Grey (LNHM); 1 female, 25° 9'S 151° 11'E, 24 km. N by E of Eidsvold, 11.x.84, I.D. Naumann and J.C. Cardale (ANIC); 1 female, 3 km. NE of Eidsvold, 11.viii.66, E.M. Exley (UQIC); 1 female, 35 km. NW of Bowen, 2.x.50, R.F. Riek (ANIC); 1 female, Mt. Boppy, 25.xi.49, E.F. Riek (ANIC). **Northern Territory**. 1 female, Macdonald Downs, 400 m., 30.x.62, E.S. Ross and D. Cavagnaro (CAS); 1 male, 11° 07'S 132° 08'E, Smith Point, Cobourg Peninsula, 10.ii.77, R.C. Lewis (ANIC); 1 female, 12° 25'S 132° 58'E, 1 km. N of Cahills Crossing (E. Alligator River), 8-9.xi.72, J.C. Cardale (ANIC); 3 females, 12° 28'S 132° 52'E, Jabaluka (=Jabiluka) Lagoon, 14 km. N of Mudginbarry HS., 14.xi.72, J.C. Cardale (ANIC); 1 female, 12° 35'S 132° 52'E, Magela Creek, 2 km. N of Mudginbarry HS., 14-15.xi.72, J.C. Cardale (ANIC); 7 females, 12° 17'S 133° 20'E, Cooper Creek, 11 km. S by W of Nimbuwah Rock, 3-4.vi.73, J.C. Cardale (ANIC); 2 females, 12° 48'S 132° 42'E, Nourlangie Creek, 8 km. N of Mt. Cahill, 19-20.xi.72, J.C. Cardale (ANIC); 2 females, 12° 48'S 132° 42'E, Nourlangie Creek, 8 km. N of Mt. Cahill, 16-17.vi.73, J.C. Cardale (ANIC); 1 female, 12° 52'S 132° 46'E, Nourlangie Creek, 6 km. E of Mt. Cahill, 8.xi.72, J.C. Cardale (ANIC); 1 female, Darwin, xi.58, N.L.H. Krauss (Bishop); 1 female, Arnhem Land, Maningrida, 19.iii.61, J.L. and M. Gressitt (Bishop); 7 females, 15° 58'S 136° 21'E, 12 km. NNE of Borroloola, 1.xi.75, J.C. Cardale (ANIC); 7 females, 16° 8'S 136° 'E, 22 km. WSW of Borroloola, 2.xi.75, J.C. Cardale (ANIC); 1 female, 16° 19'S 136° 5'E, 36 km. SW of Borroloola, 4.xi.75, J.C. Cardale (ANIC); 1 female, 16° 32'S 136° 10'E, Cattle Creek, 54 km. S by W of Borroloola, 27.x.75, J.C. Cardale (ANIC); 1 female, 16° 3'S 136° 19'E, 3 km. N by E of Borroloola, 31.x.75, J.C. Cardale (ANIC); 1 female, 16° 27'S 136 5'E, McArthur River, 48 km. SW by S of Borroloola, 29.x.75, J.C. Cardale (ANIC); 1 female, 16° 40'S 135° 51'E, Bessie Spring, 8 km. ESE of Cape Crawford, 26.x.75, J.C. Cardale (ANIC); 4 females, 19 km. N of Daly Waters, 16.xi.74, E.M. Exley and R.I. Storey (UQIC); 1 female, 17 km. N of Pine Creek, 22.xi.74, E.M. Exley and R.I. Storey (UQIC); 1 female, 17 km. N of Mataranka, 17.xi.74, E.M. Exley and R.I. Storey (UQIC); 1 female, 19 mi. ENE of Victoria River Downs HS., 18.vi.69, M. Mendum (ANIC); 1 female, 7 mi. W by S of Moolooloo OS., 18.vi.69, M. Mendum (ANIC). **Western Australia**. 3 females, 13 km. S of Carnarvon, 4.i.76, E.M. Exley and R.I. Storey (UQIC); 1 female, 16 km. E of Carnarvon, 3.i.76, E.M. Exley and R.I. Storey (UQIC); 3 females, NW Coastal H'way, 48 km. N of Murchison River Crossing, 6.i.76, E.M. Exley and R.I. Storey (UQIC); 1 female, Crossing Pool, Millstream, 23.x.70, J.C. Cardale (ANIC); 2 females, 24° 55'S 128° 48'E, 28 km. W by S of Docker River, 17.xi.77, M.S. Upton (ANIC); 2 females, Drummond Cove, 7 mi. N of Geraldton, 29.v.73, N. McFarland (LNHM); 1 female, 1 male, 20 km. W of Coolgardie, 12.ii.82, M. Powell (WAM); 1 female, Spargoville, 28 mi. W of Coolgardie, 14-15.i.36, R.E. Turner (BMNH); 2 females, Merredin, 20.i.62, G.F. Mees (WAM); 1 female, Barrow Is., ii.77, H. Heatwole and W.H. Butler (WAM); 1 female, Mt. Jackson, A.M. Douglas (WAM); 1 female, 60 km. S of Norseman, 2.i.77, A.M. and M.J. Douglas (WAM); 1 female, 16 km. N of Northampton, 21.xi.63, J. Sedlacek (Bishop). **New South Wales**. 1 female, 31° 44'S 142° 41'E, Spring Creek, 68 km. W by S of Wilcannia, 29.xi.81, J.C. Cardale and I.D. Naumann (ANIC); 2 females, 28 km. N of Bourke, 15.xii.76, E.M. Exley and T. Low (UQIC); 1 female, 34 km. SE of Moree, 30.xi.76, E.M. Exley and R.I. Storey (UQIC); 1 female, 36 W of Cobar, 11.xii.76, E.M. Exley and R.I. Storey (UQIC); 1 female, Barrigun, 11.xii.63, A.L. Dyce (ANIC). **Victoria**. 2 female, Strathmore, 1.v.58, Spurell (NMV). **South Australia**. 1 female, Orroroo, 2.viii.41 (ANIC).

Remarks. Like *B. diminuta*, the hairs on T4-6 of the females range from shorter than the width of scape and plumose to slightly longer and spiculate or plumose only at the tips. The male type has short, fuscous, erect hairs and transparent prostrate hairs.

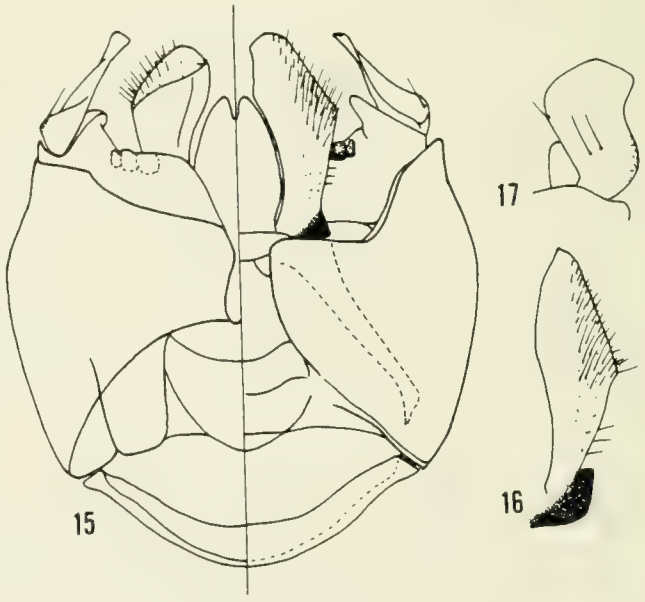
Braunsapis clarissima (Cockerell)

Allodape clarissima Cockerell, 1929a, p. 15. Type: male, Thursday Is., Queensland (NMNH).
Allodapula clarissima (Cockerell): Michener and Syed, 1962, p. 39.
Allodapula perkinsiella Michener, 1962, p. 37. Type: female, Mackay, Queensland (BMNH) (**New synonymy**). [One paratype is *B. simillima* (Smith)].

Female. Face as in Fig. 54. (1) Length 5.50 - 7.00 mm. (6) Tegula transparent to fuscous, axillary sclerites yellow to partly fuscous. (7) HW 1.56 - 1.90 mm. (8) HW/HL ratio 1.08 - 1.12. (12) Basitibial plate with carina conically raised, sometimes weak. (13) Hairs on T4-6 transparent to light brown; longer hairs suberect, simple, sometimes blunt, usually over twice as long as width of scape; shorter hairs prostrate, simple to spiculate (Fig. 97).

Male. Face as in Fig. 55. (18) HW 1.60 - 1.76 mm. (19) HW/HL ratio 1.16 - 1.18. (21) Hairs on T4-6 longer, about one and a half to twice as long as width of scape, simple. (22) Genitalia (n=2) as in Figs. 15-17; gonostylus narrowed at apex, with 1-2 setae medially, sometimes with one seta on dorso-lateral margin (Fig. 17); ventro-apical plate of gonocoxite with 3 peg-like processes; penis valve slender, mid-lateral flange absent (Fig. 16).

Specimens examined. Type as listed and the holotype and paratypes of *B. perkinsiella* from Queensland: 1 female, Rockhampton, 12.viii.58, C.D. Michener (SMUK); 2 females, Mackay, xii.99 (Turner coll.) (BMNH); 1 female, same data except (ANIC); 1 female, same data except (SMUK); 4 females, Yaamba (nest no. 20), 11.viii.58, C.D. Michener (SMUK); 6 females, 2 males, Wandoo Station, 36 mi. SW of Sarina (nest no. 16), C.D. Michener (SMUK); 1 male, same data except nest no. 14. **Queensland**. 7 females, Prince of Wales Is., Torres Strait, 27-30.v.69, Neboiss (NMV); 2 females, Prince of Wales Is., Torres Strait, 14.ii.39. R.G. Wind (AMNH); 1 female, Moa Is., Torres Strait, J.W. Schomberg (SAM); 1 female, Yaamba, near Rockhampton (nest no. 35), viii.58, C.D. Michener (SMUK); 1 female, Mackay, 19.xii.60 (ANIC); 2 females, Proserpine, 9.viii.66, J.C. Cardale (UQIC); 1 female, Cape Pallarenda, 23.viii.66, J.C. Cardale (UQIC); 3 females, 16° 24'S 144° 47'E, Kelly St. George River, 14 km. W of Mt. Desailly, 26.iv.81, I.D. Naumann (ANIC); 1 female, 16° 7'S 144° 47'E, Palmer River, 5 km. S by W of Mt. Herman, 27.ix.80, J.C. Cardale (ANIC); 1 female, Airstrip, 27 km. N of Coen, 28.vi.75, S.R. Monteith (ANIC); 1 female, 12 km. W of Fairview via Laura, 26.vi.75, S.R. Monteith (ANIC); 1 female, 25° 3'S 152°



Figs. 15-17. Male genitalia of *B. clarissima*, Mt. Brockman, 14 km. S by E of Mudginbarry, Northern Territory. **Fig. 15.** Dorsal (right) and ventral (left) view of genitalia. **Fig. 16.** Penis valve, dorso-apical view. **Fig. 17.** Gonostylus, lateral view.

14'E, 11 km. N by E of Cordalba, 9.ix.77, M.S. Upton and H. Frauca (ANIC); 1 female, 25° 22'S 151° 7'E, Eidsvold, 11.x.84, I.D. Naumann and J.C. Cardale (ANIC); 1 female, Eidsvold, x.29 - iv.30, T.L. Bancroft (ANIC); 1 female, 50 km. S of Ayr, 11.ix.50, E.F. Riek (ANIC); 1 female, Mt. Isa and vicinity, 30-31.viii.72, H.E. Evans and R.W. Matthews (MCZ); 1 female, same data except (SAM); 1 female, 20 km. N of Mt. Isa, 6.xii.74, R.I. Storey (UQIC). **Northern Territory**. 1 female, 11° 9'S 132° 9'E, Black Point, Cobourg Peninsula, 31.i.77, E.D. Edwards (ANIC); 1 female, 12° 43'S 132° 54'E, Mt. Brockmann, 14 km. S by E of Mudginbarry HS., 11-12.vi.73, J.C. Cardale (ANIC); 1 female, 12° 52'S 132° 46'E, Nourlangie Creek, 6 km. E of Mt. Cahill, 18.xi.72, J.C. Cardale (ANIC); 7 females, 12° 48'S 132° 42'E, Nourlangie Creek, 8 km. N of Mt. Cahill, 16-17.vi.73, J.C. Cardale (ANIC); 1 female, 12° 48'S 132° 42'E, Nourlangie Creek, 8 km. N of Mt. Cahill, 19-20.xi.72, J.C. Cardale (ANIC); 6 females, 12° 17'S 133° 20'E, Cooper Creek, 11 km. S by W of Nimbuwah Rock, 3-4.vi.73, J.C. Cardale (ANIC); 2 females, 12° 6'S 133° 4'E, Cooper Creek, 19 km. E by S of Mt. Borradaile, 5-6.vi.73, J.C. Cardale (ANIC); 4 females, 12° 23'S 132° 57'E, 5 km. NNW of Cahills Crossing (E. Alligator River), 8-9.vi.73, J.C. Cardale (ANIC); 1 female, 12° 52'S 132° 50'E, 15 km. E of Mt. Cahill, 6-9.iii.73, M.S. Upton (ANIC); 2 females, 12° 47'S 132° 45'E, Baroalba Creek, 11 km. NNE of Mt. Cahill, 15.xi.72, J.C. Cardale (ANIC); 1 female, 15° 58'S 136° 21'E, 12 km. NNE of Borroloola, 1.xi.75, J.C. Cardale (ANIC); 1 female, 16° 8'S 136° 6'E, 22 km. WSW of Borroloola, 2.xi.75, J.C. Cardale (ANIC); 1 female, 16° 27'S 136° 5'E, 48 km. SW of Borroloola, 29.ix.75, J.C. Cardale (ANIC); 1 female, 17 km. N of Pine Creek, 22.xi.74, E.M. Exley and R.I. Storey (UQIC); 1 female, 19 km. N of Daly Waters, 16.xi.74, E.M. Exley and R.I. Storey (UQIC); 1 female, 35 km. W of Wildman River, 26.xi.74, E.M. Exley and R.I. Storey (UQIC); 1 female, Katherine, 3.x.46 (ANIC); 1 female, 55 mi. N of Katherine, 16.iii.73, E.M. Exley (UQIC); 1 female, 6 km. SW of Katherine, 18.v.73, T.F. Houston (SAM); 3 female, Jabiru, 5-9.vi.84, I.D. Naumann (ANIC); 1 female, Stapleton, G.F. Hill (NMV); 1 female, Melville Is., G.F. Hill (SAM). **Western Australia**. 1 female, 14° 49'S 126° 49'E, Carson escarpment, 9-15.viii.75, I.F.B. Common and M.S. Upton (ANIC). **New South Wales**. 1 female, 85 km. N of Bourke, 15.xii.76, E.M. Exley and T. Low (UQIC); 1 female, 15 km. SE of Moree, 30.xi.76, E.M. Exley and T. Low (UQIC); 1 female, 36 km. W of Cobar, 11.xii.76, E.M. Exley and T. Low (UQIC).

Remarks . The type of *Allodapula perkinsiella* (BMNH) is similar to females of *B. clarissima* in having the lower half of the clypeus partly black and the longer hairs on T4-6 transparent to light brown, about twice as long as the width of the scape. The type of *Allodapula perkinsiella* has fuscous tegulae; however, this character is not very reliable, as shown by the variation in *B. unicolor* and *B. nitida* (Fig. 5). *Allodapula perkinsiella* is therefore synonymized under *B. clarissima*. The male type of *B. clarissima* is quite similar to males of *B. simillima*. *B. clarissima* differs, however, by having a slender penis valve without a mid-lateral flange (Fig. 16) and the gonostylus with 1-2 setae medially, and is smaller (HW 1.60 - 1.76 mm.) than *B. simillima*. The female of *B. clarissima* is quite similar in appearance to *B. plebeia* except for the long and simple hairs on T4-6.

The larvae described by Michener and Syed (1962) under *Allodapula perkinsiella* should be those of *B. clarissima*.

Braunsapis plumosa, n. sp.

Holotype: female, 16° 28'S 136° 9'E, 46 km SSW of Borroloola, Northern Territory, 28.x.75, J.C. Cardale (ANIC). *Paratype*: **Northern Territory**. female, Blue Painting Site, Kakadu NP, 6-8.vi.1984, I.D. Naumann (ANIC).

Female. Face as in Fig. 56. (1) Length 5.00 - 6.25 mm. (4) Paraocular mark sometimes present. (7) HW 1.70 - 1.86 mm (1.86 mm). (8) HW/HL ratio 1.06. (10) Middle of epistomal suture strongly raised. (12) Basitibial plate with carina weak. (13) Hairs on T4-6 transparent; longer hairs suberect, curved, simple to blunt, about equal to or shorter than width of scape; shorter hairs strongly plumose.

Remarks. The paratype has a small yellowish spot on the labrum and the paraocular marks are absent. This species resembles *B. plebeia* in general appearance, but it is distinguished by having the shorter hairs on T4-6 prostrate and strongly plumose.

The name *plumosa* is derived from the Latin *plumosus*, meaning feathered, referring to the strongly plumose shorter hairs on T4-6.

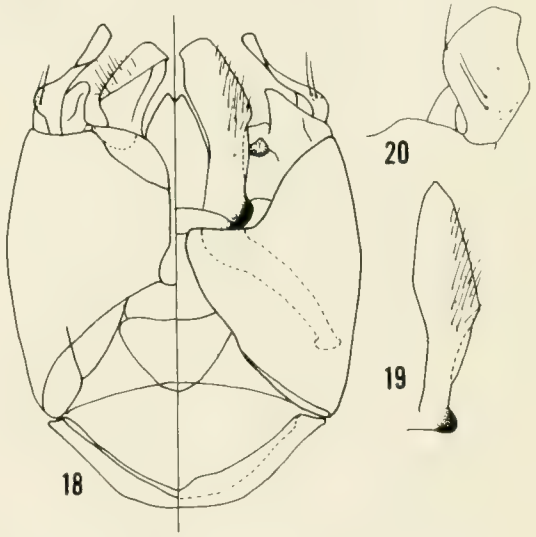
Braunsapis diminutoides, n. sp.

Holotype: female, 12° 17'S 133°20'E, Cooper Creek, 11 km. S by W of Nimbuwah Rock, Northern Territory, 3-4.vi.73, J.C. Cardale (ANIC). *Paratypes*: **Northern Territory**. 5 females, same data as holotype; 3 females, 15° 58'S 136° 21'E, 12 km. NNE of Borroloola, 1.xi.75, J.C. Cardale (ANIC); 1 female, 16° 3'S 136° 19'E, 3 km. N by E of Borroloola, 31.x.75, J.C. Cardale (ANIC); 1 female, 16° 10'S 136° 15'E, Goose Lagoon, 11 km. SW by S of Borroloola, 31.x.75, J.C. Cardale (ANIC); 1 female, 16° 27'S 136° 5'E, McArthur River, 48 km. SW by S of Borroloola, 29.x.75, J.C. Cardale (ANIC); 1 female, 12° 47'S 132° 51'E, 19 km. NE by E of Mt. Cahill, 13.vi.73, J.C. Cardale (ANIC); 1 male, Stuart H'way, 19 km. N of Katherine, 25.xi.72, D.H. Colless (ANIC).

Female. Face as in Fig. 57. (1) Length 4.50 - 6.00 mm. (7) HW 1.40 - 1.63 mm (1.44 mm). (8) HW/HL ratio 1.06 - 1.09. (12) Basitibial plate with carina conically elevated. (13) Hairs on T4-6 transparent; longer hairs slanting to suberect, simple, twice as long as width of scape; shorter hairs prostrate, spiculate.

Male. Face as in Fig. 58. Similar to that of *B. diminuta* except: (18) Head with 1.27 - 1.56 mm. (19) HW/HL ratio 1.14 - 1.16. (21) Hairs on T4-6 about one and a half to twice as long as width of scape, simple. (22) Genitalia as in Figs. 18-20; gonostylus narrowed at apex, with 2 setae medially, one seta present on dorso-lateral margin (Fig. 20); ventro-apical plate of gonocoxite asymmetrical, right plate with 3 peg-like processes, left plate with 2 peg-like processes; penis valve slender, mid-lateral flange narrow, dorso-lateral gap wider than mid-lateral flange (Fig. 19).

Remarks. This species is very similar to *B. clarissima* and distinguished from it mainly by size. The female of *B. diminutoides* is also similar to *B. diminuta* and separated from it only by having long simple hairs on T4-6, hence the name *diminutoides*. The male is



Figs. 18-20. Male genitalia of *B. diminutoides* (paratype), Stuart H'way, 19 km. N of Katherine, Northern Terriory. **Fig. 18.** Dorsal (right) and ventral (left) view of genitalia. **Fig. 19.** Penis valve, dorso-apical view. **Fig. 20.** Gonostylus, lateral view.

easily recognized by having a narrow penis valve with a small mid-lateral flange (Fig.19).

***Braunsapis anthracina*, n. sp.**

Holotype: female, 16° 35'S 122°48'E, 6 km. W Martin's Well, West Kimberly, Western Australia, 26.iv.77, D.H. Colless (ANIC). *Paratypes*: **Western Australia**. 5 females, 2 males, same data as holotype.

Female. Face as in Fig. 59. (1) Length 4.3 - 5.2 mm. (3) Clypeus black. (5) Pronotal lobe black. (6) Tegula translucent fuscous, black mesally, axillary sclerites black. (7) HW 1.36 - 1.50 mm (1.43 mm). (8) HW/HL ratio 1.04 - 1.06. (12) Basitibial plate with carina conically produced. (13) Hairs on T4-6 black; longer hairs suberect, blunt or spiculate apically, longer than width of scape; shorter hairs subprostrate, simple.

Male. Face as in Fig. 60. (14) Length 4.25 - 4.50 mm. (15) Labrum and mandible black. (16) Clypeus black. (17) Paraocular mark absent. (18) HW 1.30 - 1.33 mm. (19) HW/HL ratio 1.08. (21) Hairs on T4-6 black; longer hairs suberect, simple, usually slightly longer than width of scape; shorter hairs prostrate, simple. (22) Genitalia as in Figs. 21-23; gonostylus with moderately long seta (Fig. 23); ventro-apical plate of gonocoxite symmetrical, with 3 peg-like processes; penis valve with mid-lateral flange convex, dorso-lateral gap wider than mid-lateral flange (Fig. 22).

Remarks. This species differs from *B. minor* in having the head broader than long and differs from *B. nitida* in having the pronotal lobe black and the hind trochanter of males simple. One of the male paratypes has the longer hairs of T4-6 shorter than the width of the scape.

The name *anthracina* is derived from the Latin *anthracinus*, meaning coal-black, referring to the entirely black body color of the species.

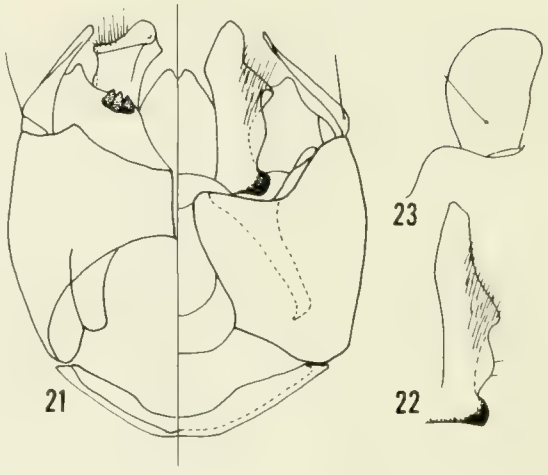
THE *VERTICALIS* SPECIES GROUP

The female in this monotypic group is similar to those of the *diminuta* species group in having a broad clypeal mark, transparent tegula and yellow axillary sclerites. The hairs on T4-6, however, are fuscous instead of transparent. Also, unlike the *diminuta* species group, the males have the trochanter lobed and both sexes have the vertex sharply declivous posteriorly (Fig. 90).

***Braunsapis verticalis*, n. sp.**

Holotype: female, 12° 48'S 132° 42'E, Nourlangie Creek, 8 km. N of Mt. Cahill, 19-20.xi.72, Northern Territory, J.C. Cardale (ANIC). *Paratypes*: **Northern Territory**. 6 females, same data as holotype; 1 female, 12° 17'S 133° 13'E, Birraduk Creek, 18 km. E by N of Oenpelli, 4-5.vi.73, J.C. Cardale (ANIC); 3 females, 12° 23'S 132° 56'E, 7 km. NW by N of Cahills Crossing (E Alligator River), 9-10.vi.73, J.C. Cardale (ANIC); 4 females, 12° 26'S 132° 58'E, Cahill Crossing (E Alligator River), 12.xi.72, J.C. Cardale (ANIC); 1 female, 1 male, 12° 31'S 132° 54'E, 9 km. N by E of Mudginbarry HS., 10-11.vi.73, J.C. Cardale (ANIC); 1 female, 12° 43'S 132° 54'E, Mt. Brockman, 14 km. S by E of Mudginbarry HS., 11-12.vi.73, J.C. Cardale (ANIC); 3 females, 12° 46'S 132° 39'E, 12 km. NNW of Mt. Cahill, 15-16.vi.73, J.C. Cardale (ANIC); 1 female, same data except 20.v.73, M.S. Upton (ANIC); 3 females, 12° 47'S 132° 51'E, 19 km. NE by E of Mt. Cahill, 13.vi.73, J.C. Cardale (ANIC); 1 female, same data except 16.xi.72 (ANIC); 9 females, 16° 8'S 136° 6'E, 46 km. SSW of Borroloola, 28.x.-2.xi.75, J.C. Cardale (ANIC); 1 female, Jabiru, 5-9.vi.84, I.D. Naumann (ANIC); 1 male, 12° 50'S 132° 51'E, 16 km. E by N of Mt. Cahill, 13.vi.73, J.C. Cardale (ANIC); 9 females, 2 males, 11° 1'S 136° 45'E, Rimbija Is., Wessel Islands, 14.i.77, E.D. Edwards (ANIC).

Female. Face as in Fig. 61. (1) Length 6.0 - 7.0 mm. (2) Labrum and mandible black. (3) Lower half of clypeus partly black. (4) Paraocular mark absent. (5) Pronotal lobe yellow. (6) Tegula transparent, axillary sclerites yellow. (7) HW 1.80 - 2.20 mm (1.96 mm). (8) HW/HL ratio 1.10 - 1.14. (9) Malar space shorter than width of scape. (10) Middle of epistomal suture strongly raised. (11) Scape reaching front ocellus, sometimes posterior ocelli. (12) Basitibial plate with carina weak. (13) Hairs on T4-6 fuscous; longer hairs curved, spiculate dorsally, longer than width of scape; shorter hairs prostrate, simple (Fig. 96).



Figs. 21-23. Male genitalia of *B. anthracina* (paratype), 6 km. W of Martin's Well, West Kimberly, Western Australia. **Fig. 21.** Dorsal (right) and ventral (left) view of genitalia. **Fig. 22.** Penis valve, dorso-apical view. **Fig. 23.** Gonostylus, lateral view.

Male. Face as in Fig. 62. (14) Length 5.80 - 6.50 mm. (15) Labrum yellow, mandible black. (16) Clypeus yellow. (17) Paraocular mark present. (18) HW 2.00 - 2.10 mm. (19) HW/HL ratio 1.18 - 1.22. (20) Hind trochanter notched and lobed. (21) Hairs on T4-6 fuscous to black; longer hairs slanting, thick, tapering at apex, slightly longer than width of scape; shorter hairs prostrate, simple. (22) Genitalia as in Figs. 24-26; gonostylus broad basally, tapering apically, with five setae medially, one seta dorso-laterally (Fig. 26); ventro-apical plate of gonocoxite symmetrical, with 3 peg-like processes; penis valve with mid-lateral flange broad, dorso-lateral gap about twice as wide as mid-lateral flange (Fig. 25).

Remarks. This species is distinctive in having the vertex sharply declivous posteriorly, almost carinate, with a wide shallow depression just behind the posterior ocelli, coarsely and densely punctate on vertex (Fig. 90).

The name *verticalis* refers to the carinate area on the vertex.

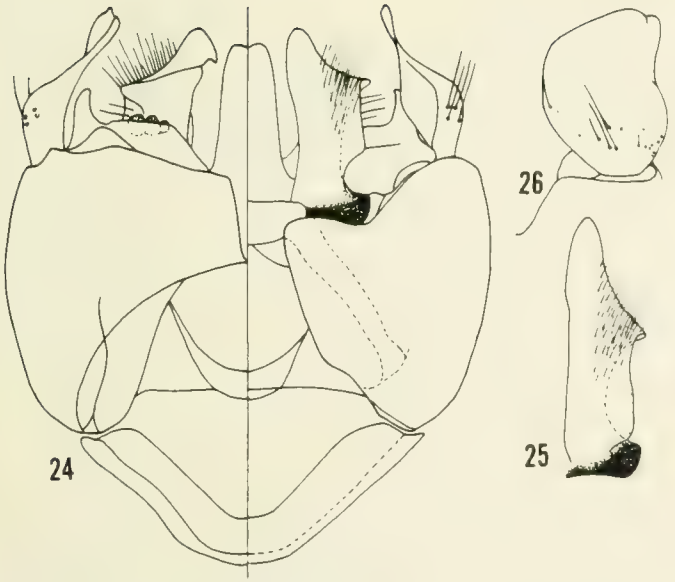
THE *SIMILLIMA* SPECIES GROUP

This group is characterized by the following characters: hairs on T4-6 fuscous to black; head broader than long; males with hind trochanter lobed. Except for *B. simillima*, the females of this group usually have the clypeal mark slender, strongly tapering towards the apex as in Figs. 66, 70, 72.

***Braunsapis simillima* (Smith)**

Allodape simillima Smith, 1854, p. 229. Type: female, Macintyre River, New South Wales (BMNH).

Allodapula simillima (Smith): Michener and Syed, 1962, pp. 22-23, 36-37; Michener, 1965, p. 223.



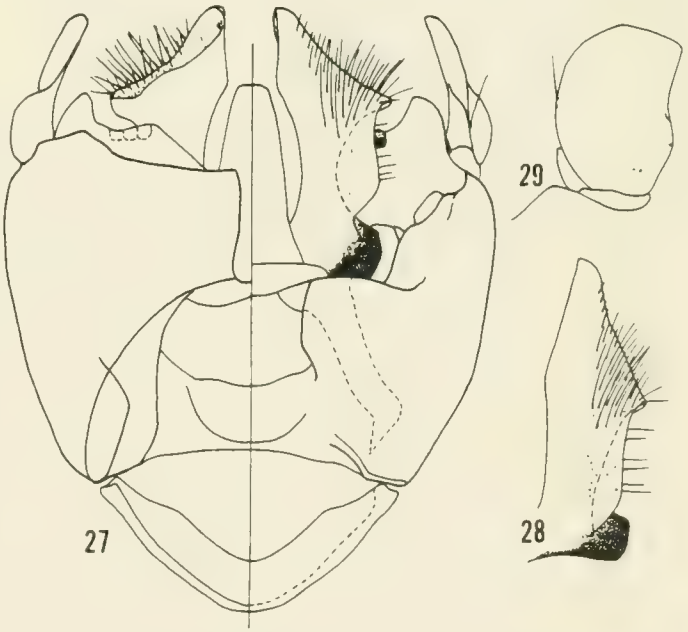
Figs. 24-26. Male genitalia of *B. verticalis* (paratype), Rimbija Is., Wessel Is., Northern Teritory. **Fig. 24.** Dorsal (right) and ventral (left) view of genitalia. **Fig. 25.** Penis valve, dorso-apical view. **Fig. 26.** Gonostylus, lateral view.

Allodapula perkinsiella Michener: Michener and Sved, 1962, pp. 33-34, 37; Michener, 1965, p. 223 (in part, 1 paratype).
Allodape plebeia Cockerell, 1929b, p. 15 [female cotype (=paratype) only].

Female. Face as in Fig. 63. (1) Length 5.00 - 9.00 mm. (2) Labrum and mandible black. (3) Lower half of clypeus partly black. (4) Paraocular mark absent. (5) Pronotal lobe yellow. (6) Tegula transparent to fuscous, axillary sclerites yellow, mixed or dark. (7) HW 1.76 - 2.36 mm. (8) HW/HL ratio 1.10 - 1.14. (9) Malar space shorter than width of scape. (10) Middle of epistomal suture slightly raised. (11) Scape reaching front ocellus. (12) Basitibial plate with carina strongly raised, rarely weak. (14) Hairs on T4-6 fuscous to black; longer hairs suberect, simple, slightly longer than the width of scape; shorter hairs subprostrate, simple.

Male. Face as in Figs. 64-65. (14) Length 5.30 - 7.80 mm. (15) Labrum and mandible yellow, latter sometimes only partly. (16) Clypeus yellow. (17) Paraocular mark present. (18) HW 1.90 - 2.23 mm. (19) HW/HL ratio 1.16 - 1.20. (20) Hind trochanter notched and lobed, yellow at tip. (21) Hairs on T4-6 fuscous to black; longer hairs suberect, simple, longer than width of scape; shorter hairs slanting or subprostrate, simple. (22) Genitalia (n = 5) as in Figs. 27-29; gonostylus with short seta (Fig. 29); ventro-apical plate of gonocoxite either symmetrical or asymmetrical, right plate with 3-5 peg-like processes, left plate with 3-4 peg-like processes; penis valve with mid-lateral flange broad, dorso-lateral gap wider than mid-lateral flange (Fig. 28).

Specimens examined. Type as listed. **New Guinea**. 1 female, SE of Cape Rodney, 4.xi.60, J.L. and M. Gressitt (Bishop); 1 female, Mobitei, 750 m., NE Torricelli Mts., 16-22.iv.59, W.W. Brandt (Bishop); 1 female, Ginnakan, Hollandia area, 50 m., West New Guinea, 13.vii.57, D.E. Hardy (Bishop). **Queensland**. 8 females, Prince of Wales Is., Torres Strait, 14.ii.39, R.G. Wind (CAS); 2 females, same data except (SMUK); 2 females, same data except (AMNH); 2 females, Prince of Wales Is., Torres Strait, 27-30.v.69, Neboiss (NMV); 3 females, Coen, Cape York, 25.v.52, Darlington (MCZ); 1 female, Mackay, iv.99 (LNHM); 1 female, Mareeba, 25.xii.50 (NMV); 1 female, Mt. Nebo, 23.xi.57, J. Kerr (NMV); 1 male, Mt. Cootha, 23.viii.55, J. Kerr (NMV); 1 female, Kuranda, 10.ix.50 (A.N. Burns coll.) (NMV); 1 female, 30 mi. W of Collinsville, 12.ix.50, E.F. Riek (ANIC); 2 females (1 paratype of *B. perkinsiella*), Collinsville, 15-16.ix.50, E.F. Riek (ANIC); 6 females, 10 S of Bowen, 27.ix.50, E.F. Riek (ANIC); 9 females, 36 mi. SW by S of Mt. Garnet, 19.iv.69, I.F.B. Common and M.S. Upton (ANIC); 1 female, Eidsvold, 8.ix.20 (ANIC); 1 female, 16° 7'S 144° 47'E, Palmer River, 5 km. S by W of Mt. Herman, 27.ix.80, J.C. Cardale (ANIC); 1 male, Mt. Walsh National Park, Biggenden, viii.72, H. Frauca (ANIC); 1 female, 2 males, Bluff Range, Biggenden, 1-19.xii.71, H. Frauca (ANIC); 1 female, South Slope, Bluff Range, Biggenden, 15.viii.73, H. Frauca (ANIC); 1 female, Coast Range, near Biggenden, 23.xi.75, H. Frauca (ANIC); 1 female, Coast Range, 10-12 km. S by E of Biggenden, 12-13.xii.77, H. Frauca (ANIC); 1 male, Pinnacles, Bluff Range via Biggenden, 1.x.74, H. Frauca (ANIC); 1 male, Double-Sloping Hummock via Rosedale, 27.x.74, H. Frauca (ANIC); 1 male, South Boolboonda range via Mt. Perry, 10.x.73, H. Frauca (ANIC); 3 females, sandstone outcrops, 30 km. W of Fairview via Laura, 22-24.vi.76, G.B. and S.R. Monteith (ANIC); 1 male, Stradbroke Is., 17.ix.15, H. Hacker (QM); 1 female, Brisbane, 9.iv.11, H. Hacker (NMNH); 1 female, Beerwah, 29.viii.58, C.D. Michener (SMUK); 1 female, Morven, 31.x.71, E.M. Exley (UQIC); 1 female, Ban-Ban Range via Coalstoun Lakes, i.74, H. Frauca (ANIC); 1 female, Archer Creek, 15 km. W by S of Ravenshoe, 20.v.80, I.D. Naumann and J.C. Cardale (ANIC); 4 females, 15° 6'S 145° 14'E, 12-14 km. ESE of Mt. Webb, 3.x.80, J.C. Cardale (ANIC); 1 female, 15° 17'S 145° 13'E, 1 km. N of Rounded Hill, 5-7.v.81, I.D. Naumann (ANIC); 1 female, W of Condamine, 20.xi.66, T.F. Houston (SAM); 1 female, 17 mi. N of Rockhampton, 11.viii.67, T.F. Houston (SAM); 1 female, Acacia Ridge, 21.viii.66, T.F. Houston (SAM); 1 female, 2 males, Pamicestone, near Beerburrum, 29.vi.66, T.F. Houston (SAM); 1 male, Mt. Beerburrum, 4.ix.67, T.F. Houston (SAM); 2 males, Tibrogargan Creek, 4.ix.67, T.F. Houston (SAM); 1 male, 30 mi. N of Miles, 30.ix.67, T.F. Houston (SAM); 2 males, Murphy Creek, 30.ix.67, J.C. Cardale (UQIC); 1 male, Cape Pallarenda, 19.viii.66, J.C. Cardale (UQIC); 1 male, Tin Can Bay, 21.viii.57, F.A. Perkins (UQIC). **Northern Territory**. 3 females, 12° 50'S 132° 52'E, 19 km. E by N of Mt. Cahill, 14.vi.73, J.C. Cardale (ANIC); 2 females, 12° 52'S 132° 47'E, Nourlangie Creek, 8 km. N of Mt. Cahill, 14-15.vi.73, J.C. Cardale (ANIC); 2 females, same data except 17-18.xi.72; 1 female, 12° 48'S 132° 42'E, Nourlangie Creek, 8 km. N of Mt. Cahill, 16-17.vi.73, J.C. Cardale (ANIC); 1 female, Nourlangie Creek, 6 km. E of Mt. Cahill, 18.xi.72, J.C. Cardale (ANIC); 1 female, 12° 52'S 132° 50'E, Koongarra, 15 km. E of Mt. Cahill, 12-13.vi.73, J.C. Cardale (ANIC); 3 females, 12° 52'S 132° 50'E, 15 km. E of Mt. Cahill, 6-9.iii.73, M.S. Upton (ANIC); 1 female, 12° 40'S 132° 54'E, Magela Creek, 9 km. SSE of Mudginbarry HS., 7-8.xi.72, J.C. Cardale



Figs. 27-29. Male genitalia of *B. simillima*, Bluff Range, Biggenden, Queensland. **Fig. 27.** Dorsal (right) and ventral (left) view of genitalia. **Fig. 28.** Penis valve, dorso-apical view. **Fig. 29.** Gonostylus, lateral view.

(ANIC); 2 females, 12° 43'S 132° 54'E, Mt. Brockman, 14 km. S by E of Mudginbarry HS., 11-12.vi.73, J.C. Cardale (ANIC); 1 female, 129 mi. S of Darwin, 13.iii.73, E.M. Exley (UQIC); 2 females, Darwin, 8-9.xii.63 - 8.i.64, J. Sedlacek (Bishop); 2 females, Darwin, 2-4.xii.88, R.R. Snelling and J. Grey (LNHM); 1 female, Darwin, G. Hill (BMNH); 1 female, 16° 8'S 136° 6'E, 22 km. WSW of Borroloola, 2.xi.75, J.C. Cardale (ANIC); 1 female, 15 km. SE of Timber Creek on Victoria Highway, 20.iv.80, G. Anderson and D. Symon (WAM). **Western Australia**. 2 females, 14° 49'S 125° 50'E, Mining Camp, Mitchell Plateau, 9-19.v.83, I.D. Naumann and J.C. Cardale (ANIC); 3 females, 14° 34'S 125° 48'E, 5 km.W of Walsh Point, 10.v.83, I.D. Naumann and J.C. Cardale (ANIC); 1 female, Cockatoo Is., 18.vi.79, R. Easton (WAM); 1 female, 2 km. S of Fern Creek, Kimberly Div., 11.iv.80, G. Anderson and D. Symon (WAM). **New South Wales**. 1 female, Mt. Kaputar, 5.ix.62, C.W. Frazier (ANIC). **South Australia**. 6 females, 2 males, Orroroo, 2.viii.42 (ANIC).

Remarks. The type of *B. simillima* (BMNH) has the clypeal mark gradually tapering towards the apex, the tegula fuscous mesally, translucent fuscous along the outer margin, the axillary sclerites yellow and the carina bordering the basitibial plate weak. The female paratype of *B. plebeia* differs from the type of *simillima* by having a transparent tegula. It was wrongly associated with the male type of *B. plebeia*. *B. simillima* can be readily recognized by the broad clypeal mark (Fig. 63) and by having the area just above the mark not as raised as in *B. protuberans* (Fig. 89). The lobe on the hind trochanter of males is relatively larger and carinate on the inner side in *B. protuberans*, unlike *B. simillima*.

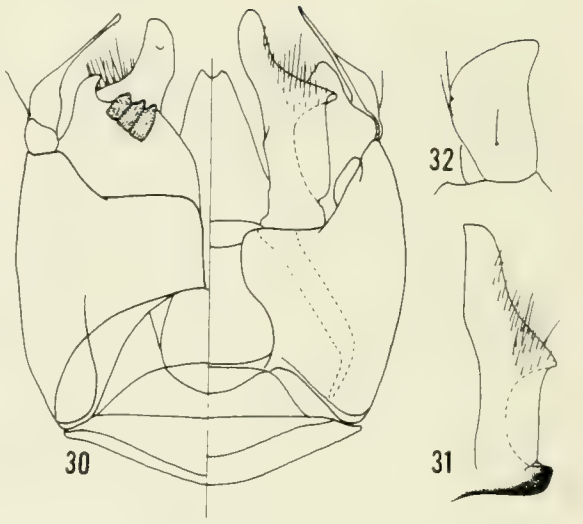
Braunsapis boharti (Krombein), new status

Allodapula mindanaonis boharti Krombein, 1951, p. 294. Type: female, Tenaru River, Guadalcanal, Solomon Islands, i.1945, G.E. Bohart (CAS); Michener and Syed, 1962, p. 36; Michener, 1965, p. 233.

Female. Face as in Fig. 66. (1) Length 6.0 - 7.3 mm. (2) Labrum black, mandible with yellow basal spot. (3) Lower half of clypeus partly black, clypeal mark narrow, strongly tapering towards apex. (4) Paraocular mark present. (6) Tegula transparent to translucent fuscous, axillary sclerites yellow. (7) HW 1.73 - 2.00 mm. (8) HW/HL ratio 1.08 - 1.14. (10) Middle of epistomal suture raised. (12) Basitibial plate with carina weak. (13) Hairs on T4-6 fuscous; longer hairs suberect, simple to blunt, shorter than width of scape; shorter hairs subprostrate, simple.

Male. Face as in Fig. 67. (14) Length 5.8 - 6.0 mm. (15) Labrum black, mandible yellow. (16) Clypeus mainly black, sometimes upper half with small yellow fleck, lower half with small spot near apical margin. (18) HW 1.67 - 1.79 mm. (19) HW/HL ratio 1.16 - 1.17. (21) Hairs on T4-6 fuscous; longer hairs suberect, simple, shorter than width of scape; shorter hairs subprostrate, simple. (22) Genitalia (n = 2) as in Figs. 30-32; gonostylus with short seta medially, with 1-2 setae dorso-laterally (Fig. 32); ventro-apical plate of gonocoxite symmetrical, with 3 peg-like processes; penis valve with mid-lateral flange broad, dorso-lateral gap wider than mid-lateral flange (Fig. 31).

Specimens examined. Type as listed. **Solomon Islands**. 1 female (paratype), Tenaru River, Guadalcanal, i.45, G.E. Bohart (NMNH); 1 male, Honiara, Guadalcanal, 0-200 m., i.73, N.L.H. Krauss (SMUK); 1 female (paratype) Russell Is., G.E. Bohart, 20.iv.45 (NMNH); 1 female, Simba Mission, Bougainville Is., 2.vii.56, E.J. Ford Jr (Bishop); 1 female, Kolotuve, Sakapisu, Santa Ysabel Is., 20,vi.60, C.W. O'Brien (Bishop); 2 females, same data except (SMUK); 1 female, Tamatahi, Santa Ysabel Is., 450 m., 3.vii.60, C.W. O'Brien (Bishop); 3 females, Gizo, Gizo Is., 0-200 m., xii.75, N.L.H. Krauss (Bishop); 1 female, Gizo, Gizo Is., 0-100 m., xi.70, N.L.H. Krauss (Bishop); 1 female, 1 male, Gizo Is., New Georgia Group, 100 m., 20.vii.64, J. and M. Sedlacek (Bishop); 2 females, Giso, New Maura, 0-50 m., xi.75, N.L.H. Krauss (Bishop); 1 female, Minda, New Georgia, 0-200 m., xi.75, N.L.H. Krauss (Bishop); 2 female, 1 male, Kira Kira, San Cristobal Is., 28.vii.60, C.W. O'Brien (Bishop); 1 female, Mono Is., 100 m., 6-11.xi.80, J.L. Gressitt (Bishop); 1 female, Bethlehem, Ndai Is., 0-10 m., xii.72, N.L.H. Krauss (Bishop); 1 female, Auki, Malaita Is., 2-20 m., 3.x.57, J.L. Gressitt (Bishop); 3 females, 1 male, Auki, Malaita Is., 0-100 m., xii.75, N.L.H. Krauss (Bishop).



Figs. 30-32. Male genitalia of *B. boharti*, Honiara, Guadalcanal, Solomon Is. **Fig. 30.** Dorsal (right) and ventral (left) view of genitalia. **Fig. 31.** Penis valve, dorso-apical view. **Fig. 32.** Gonostylus, lateral view.

Remarks. This is the only species with the hairs on the hind tibia fulvous. It is closely allied to *B. mindanaonis* described from the Philippines and was therefore placed as a subspecies by Krombein (1951). However, the color and form of hairs on T4-6 and the hind tibia are distinct enough to warrant specific status; intermediate populations are unknown.

Braunsapis protuberans, n. sp.

Allodapula perkinsiella Michener and Syed, 1962, p. 33-34, 37 (in part, 2 female paratypes).

Holotype: female, 18° 59'S 146° 2'E, 2 km. E by S of Hidden Valley, Queensland, 12.v.80, I.D. Naumann and J.C. Cardale (ANIC). *Paratypes*: **Queensland**. 2 females, same data as the holotype; 1 female, Ellis Beach, N of Cairns, 21.iv.67, D.H. Colless (ANIC); 6 females, 15° 14'S 145° 7'E, 7 km. N of Hope Vale Mission, 4.x.80, J.C. Cardale (ANIC); 7 females, 15° 17'S 145° 10'E, 5 km. W by N of Rounded Hill nr. Hope Vale Mission, 7.x.80, J.C. Cardale (ANIC); 4 females, 15° 17'S 145° 13'E, 1 km. N of Rounded Hill nr. Hope Vale Mission, 5-6.x.80, J.C. Cardale (ANIC); 9 females, 15° 10'S 145° 7'E, 3.5 km. SW by S of Mt. Baird, 3-5.v.81, I.D. Naumann (ANIC); 8 females, 15° 3'S 145° 15'E, 4 km. SW of Casuarina Hill, 30.iv-2.v.81, I.D. Naumann (ANIC); 2 females, 15° 29'S 145° 16'E, Mt. Cook Nat. Park, Cooktown, 11-12.x.80, J.C.Cardale (ANIC); 1 female, 15° 3'S 145° 9'E, 3 km. NE of Mt. Webb, 1-3.x.80, J.C. Cardale (ANIC); 2 females, Coast Range via Biggenden, 12-13.xii.77, H. Frauca (ANIC); 1 female, 26° 1'S 153° 1'E, Carland Creek, 12.x.84, I. Naumann and J.C. Cardale (ANIC); 1 female, Bluff Range, Biggenden, 1-19.xii.71, H. Frauca (ANIC); 1 female, 36 mi. SW by S of Mt. Garnet, 2500 ft., 19.iv.69, I.F.B. Common and M.S. Upton (ANIC); 1 female, Somerset, Cape York, 16-17.iv.73, S.R. Monteith (ANIC); 1 female, Pinnacle Creek, 27 km. N of Archer River Crossing, Cape York Pen., 29.vi.75, S.R. Monteith (ANIC); 7 females, 1 male, Bundaberg, viii-ix.71-72, H. Frauca (ANIC); 2 females, 4 km. N Bundaberg, ix.72, H. Frauca (ANIC); 1 male, Watalgan Range, 35 mi. NWN of Bundaberg (ca. 1500 ft.) x.1971, H. Frauca (ANIC); 1 female, 1 male, Mt. Walsh Nat. Pk. via Biggenden, 21.i.80, H. Frauca (ANIC); 11 females, Mackay (including 1 female paratype *Allodapula perkinsiella* Michener) (BMNH); 1 female, Halifax,

17.vi.19, F.X. Williams (NMNH); 2 females, Townsville, 24.ii.03, F.P. Dodd (NMNH); 1 female, Halifax, 17.vi.1919, F.X.W. (MCZ); 11 females, 1 male, Stradbroke, 13-21.ix.54, G.B. (A.N. Burns Coll.) (NMV); 7 females, 1 male, Kuranda, 10-17.ix.50, G.B. (A.N. Burns Coll.) (NMV); 1 female, Kuranda, 28.xii.49, G.B. (A.N. Burns Coll.) (NMV); 3 females, Mareeba, 23.i.55, G.B. (A.N. Burns Coll.) (NMV); 1 female, Mareeba, 21.vii.50, G.B. (A.N. Burns Coll.) (NMV); 3 females, Silver Valley, 24.ix.50, G.B. (A.N. Burns Coll.) (NMV); 3 females, Mt. Nebo, 23.xi.57, J. Kerr (A.N. Burns Coll.) (NMV); 2 males, Kuranda, 2.i.53, G.B. (A.N. Burns Coll.) (NMV); 4 males, Mt. Cootha, 24.viii.55, J. Kerr (A.N. Burns Coll.) (NMV); 1 male, Mt. Cootha, 9.x.54, J. Kerr (A.N. Burns Coll.) (NMV); 1 male, Stradbroke Is., 7-8.iv.67, J.C. Cardale (UQIC); 1 male, Stradbroke Is., 6.v.66, J.C. Cardale (UQIC); 1 male, Nambour, 31.x.54, J. Kerr (A.N. Burns Coll.) (NMV); 1 male, 15° 6'S 145° 14'E, 12-14 km. ESE of Mt. Webb, 3.x.80, J.C. Cardale (ANIC); 1 male, Beerwah, 2.x.66, T.F. Houston (SAM); 1 male, Stradbroke Is., 24.iv.66, T.F. Houston (SAM).

Female. Face as in Fig. 68. (1) Length 6.0 - 9.5 mm. (3) Lower half of clypeus partly black, clypeal mark narrow, tapering toward apex. (6) Tegula fuscous, axillary sclerites fuscous, mixed or yellow. (7) HW 1.90 - 2.37 mm (2.03 mm). (8) HW/HL ratio 1.09 - 1.14. (10) Middle of epistomal suture strongly raised, somewhat conical. (12) Basitibial plate strongly raised. (13) Hairs on T4-6 fuscous to black; longer hairs suberect, simple to blunt, equal to or longer than width of scape; shorter hairs subprostrate, simple.

Male. Face as in Fig. 69. (14) Length 5.80 - 7.50 mm. (15) Labrum with yellowish mark, mandible black. (17) Paraocular mark present, almost reaching upper level of clypeal mark. (18) HW 1.80 - 2.23 mm. (19) HW/HL ratio 1.18 - 1.20. (21) Hairs on T4-6 black; longer hairs suberect, simple, longer than width of scape; shorter hairs subprostrate to slanting. (22) Genitalia (n = 3) as in Figs. 33-35; gonostylus slightly narrowing at apex, with three short setae medially, one seta on dorso-lateral margin (Fig. 35); ventro-apical plate of gonocoxite symmetrical ; penis valve with mid-lateral flange broad, dorso-lateral gap wider than mid-lateral flange (Fig. 34).

Additional specimens examined. Types as listed. **New Guinea**. 1 female, Roku, Central Dist., Papua, 25.iv.59, C.D. Michener (Bishop). **Queensland**. 8 females, Prince of Wales Is., 14.ii.39, R.G. Wind (CAS); 2 females, same data except (SMUK); 2 females, same data except (AMNH); 1 female (paratype of *A. perkinsiella* Michener), Gladstone, 13.viii.58, C.D. Michener (SMUK); 1 female, Mackay, iii.00, Turner Coll. (LNHM); 1 female, 18 mi. N of Cairns, 13.v.70, R. and S. Matthews (MCZ); 1 female, 10 km. N of Wangeti, 19.xii.88, R.R. Snelling and J. Grey (LNHM).

Remarks. The species is easily recognized by having the middle of the epistomal suture elevated somewhat conically. Furthermore, the male gonostylus has four setae while *B. simillima* has at most only two setae. The nests nos. 40 and 95 studied by Michener and Syed (1962) and the larvae described as *B. simillima* belong to this species.

The name of this species comes from the Latin *protuberans*, meaning swelling or protuberance, referring to the condition of the middle of the epistomal suture.

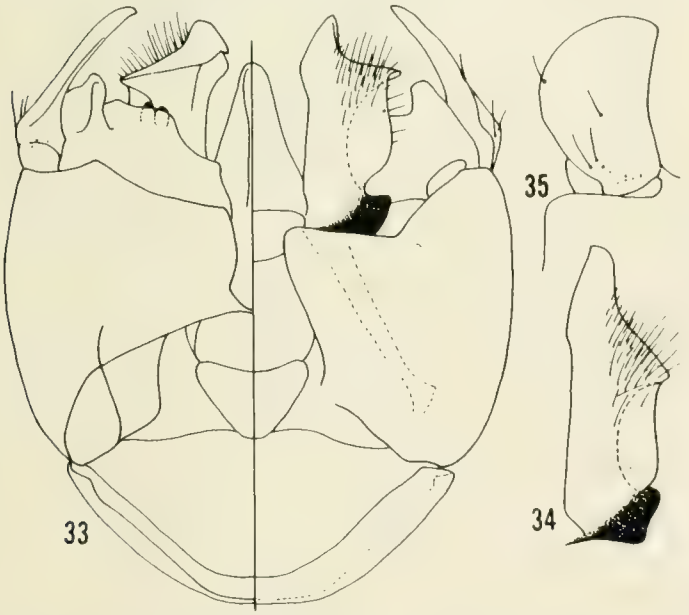
Braunsapis unicolor (Smith)

Allodape unicolor Smith, 1854, p. 230. Type: female, New Holland (=Australia) (BMNH).

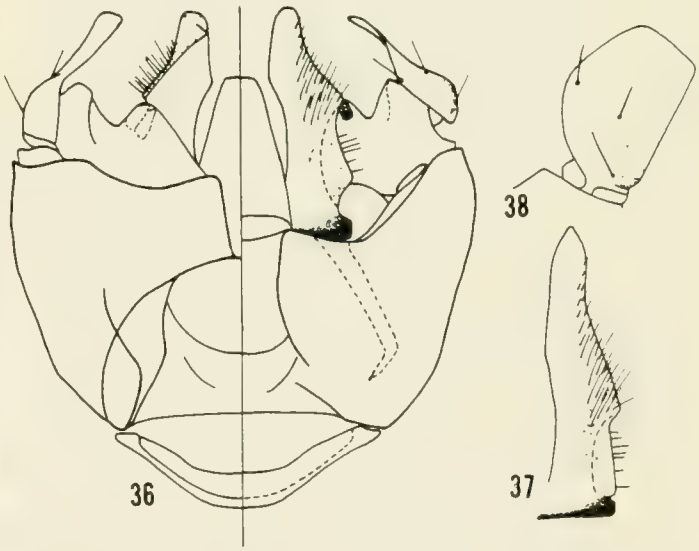
Allodapula unicolor (Smith): Michener and Syed, 1962, pp. 31-32, 38; Michener, 1965, p. 233.

Female. Face as in Fig. 70. (1) Length 3.50 - 6.50 mm. (2) Labrum and mandible black. (3) Lower half of clypeus partly black, clypeal mark narrow, strongly tapering toward apex. (7) HW 1.57 - 1.93 mm. (8) HW/HL ratio 1.06 - 1.10. (9) Malar space shorter than width of scape. (10) Middle of epistomal suture slightly raised. (12) Basitibial plate with carina raised, sometimes weak. (13) Hairs on T4-6 black; longer hairs slanting, simple to spiculate, about as long as width of scape; shorter hairs subprostrate, simple to spiculate.

Male. Face as in Fig. 71. (14) Length 3.50 - 6.00 mm. (15) Labrum yellow, sometimes only partly, mandible yellow. (16) Clypeus yellow, clypeal mark narrow at base, broader on apical half. (17) Paraocular mark absent or with small spots or elongate marks. (18) HW 1.63 - 1.86 mm. (19) HW/HL ratio 1.16 - 1.18. (21) Hairs on T4-6 fuscous to black; longer hairs suberect, simple, longer than width of scape; shorter hairs subprostrate to slanting, simple. (22) Genitalia (n = 5) as in Figs. 36-38; gonostylus with 1-3 short setae (Fig. 38); ventro-apical plate of gonocoxite either symmetrical or



Figs. 33-35. Male genitalia of *B. protuberans* (paratype), Mt. Walsh National Park via Biggenden, Queensland. **Fig. 33.** Dorsal (right) and ventral (left) view of genitalia. **Fig. 34.** Penis valve, dorso-apical view. **Fig. 35.** Gonostylus, lateral view.



Figs. 36-38. Male genitalia of *B. unicolor*, 12-14 km. ESE of Mt. Webb, Queensland. **Fig. 36.** Dorsal (right) and ventral (left) view of genitalia. **Fig. 37.** Penis valve, dorso-apical view. **Fig. 38.** Gonostylus, lateral view.

asymmetrical, with 2-4 peg-like processes; penis valve slender, dorso-lateral gap wider than mid-lateral flange (Fig. 37).

Specimens examined. Type as listed. **New Guinea**. 2 females, 2 males, Port Moresby, Papua, 25.iv.59, C.D. Michener (SMUK); 15 males, same data except (Bishop); 1 female, 25 mi. radius of Port Moresby, Papua, vi.28, Pemberton, (Bishop); 2 females, 2 males, Roku, Central District, Papua, 23.iv.59, C.D. Michener (SMUK); 2 females, Brown River, Papua, 23.x.60, J.L. Gressitt (Bishop); 1 female, Kerema, Papua, 3-9.v.59, C.D. Michener (Bishop); 2 females, Subitana, Musgrove Dist., Papua, 26.iv.59, C.D. Michener (Bishop); 6 females, 5 males, Seleo, Biró (Budapest); 1 female, same data except Simbang; 2 females, N.E. Maprik, 150 m., 29.xii-17.i.60, T.C. Maa (Bishop); 1 male, Biak Airport, 19-24.v.59, T.C. Maa (Bishop); 1 female, Nabire, S of Geelvink Bay, West New Guinea, 3.vii.62, J.L. Gressitt (Bishop); 1 female, Karadan, 24.vii.59. W.W. Brandt (Bishop). **Queensland**. 11 females, Prince of Wales Is., 14.ii.39, R.G. Wind (CAS); 4 females, 10° 12'S 142° 49'E, Warraber (Sue) Is., 8-10.xii.77, E.D. Edwards (ANIC); 5 females, Iron Range, Cape York Peninsula, 29.iv - 4.v.68, S.R. Monteith (UQIC); 2 females, Lockerbie Area, Cape York, 13-17.iv.73, S.R. Monteith (ANIC); 2 females, Somerset, Cape York, 16-17.iv.73, S.R. Monteith (ANIC); 2 females, Brown Lake, Stradbroke Is., 16.ix.81, M.A. Schneider (UQIC); 1 female, Dunwich, Stradbroke Is., 21.viii.58, C.D. Michener (SMUK); 1 female, Dunwich, 7-8.v.66, J.C. Cardale (UQIC); 1 male, Stradbroke Is., 17.ix.15, H. Hacker (QM); 1 female, 1 male, Noah Beach, Cape Tribulation NP, 18.xii.88, R.R. Snelling and J. Grey (LNHM); 1 female, Kuranda, 1916-17, F.P. Dodd (BMNH); 1 female, Barron Waters, v.46 (NMV); 1 female, Fitzroy Is., 13.v.57 (NMV); 1 female, Eubenangee, 16.x.49 (NMV); 1 female, Beerwah, 7.viii.66, T.F. Houston (SAM); 5 females, Tibrogargan, near Beerwah, 24.xi.58, C.D. Michener (SMUK); 2 females, Tibrogargan Creek, 2.viii - 4.ix.67, T.F. Houston (SAM); 2 females, 3 males, Glenmorgan, 22.x.58, C.D. Michener (SMUK); 1 female, Mutdapilly, 9.xi.58, C.D. Michener (SMUK); 3 females, Wandoo, 36 mi. SW of Sarina, 10.viii.58, C.D. Michener (SMUK); 3 females, 1 male, Yaamba, 11.viii.58, C.D. Michener (SMUK); 1 female, Magnetic Is. off Townsville, 5-7.v.70, R. and J. Matthews (MCZ); 1 female, Ravenshoe, 16.xii.88, R.R. Snelling and J. Grey (LNHM); 1 female, Burleigh, 16.ix.60, A.N. Burns (NMV); 1 female, 1 male, Mt. Coot-tha, 9.x.54 - 24.viii.55, J. Kerr (NMV); 1 female, Halifax, 17.vi.19, F.X. Williams (MCZ); 1 female, NE of Clermont, 1.xi.77, E.M. Exley and T. Low (UQIC); 4 females, Edungalba, 15.vii - 12.xii.40 (ANIC); 1 male, 15° 06'S 145° 14'E, 12-14 km ESE of Mt Webb, 3.x.80, J.C. Cardale (ANIC); 1 female, 15° 14'S 145° 7'E, 7 km. N of Hope Vale Mission, 5.x.80, J.C. Cardale (ANIC); 1 female, 15° 17'S 145° 10'E, 7 km. ENE of Hope Vale Mission, 5.x.80, J.C. Cardale (ANIC); 2 females, 15° 17'S 145° 16'E, 1 km. N of Rounded Hill near Hope Vale Mission, 5-6.x.80, J.C. Cardale (ANIC); 1 female, 15° 29'S 145° 16'E, Mt. Cook National Park, Cooktown, 11-12.x.80, J.C. Cardale (ANIC); 2 females, 15° 47'S 145° 14'E, Shiptons Flat, 17-19.x.80, J.C. Cardale (ANIC); 1 female, 17° 41'S 145° 26'E, Millstream Falls National Park, 24-25.v.80, I.D. Naumann and J.C. Cardale (ANIC); 1 female, 18° 59'S 146° 2'E, 2 km. E by S of Hidden Valley, 12.v.80, I.D. Naumann and J.C. Cardale (ANIC); 1 female, Brisbane, 20.ix.61, J. Bryan (UQIC); 3 females, 2 males, Brisbane, 14.x.13 - 26.ix.16, H. Hacker (QM); 1 female, 1 male, Brisbane, 24.iv.55, J. Kerr (NMV); 1 female, Highvale, 14 mi. NW of Brisbane, 24.i.69, R. Straatman (ANIC); 1 female, Mackay, iii.00 (NMNH); 1 female, Mackay, 17.iii.28 (NMV); 1 male, Mackay, 2.viii.29, A.N. Burns (NMV); 8 females, Mackay, x.99 - iii.00 (SMUK); 10 females, same data except (BMNH); 1 female, Expedition Range, 22.ix.73, J.C. Lisojif (ANIC); 1 female, same data except (UQIC); 1 male, Landsborough, 28.x.65, J. Cardale (UQIC); 1 female, 28 km. NW of Mundubbera, 11.iii.76, E.M. Exley (UQIC); 1 female, 2 mi. N of Mareeba, 26.x.67, E.M. Exley (UQIC); 1 female, Caloundra, 17.xii.55 (NMV); 1 female, 27.xii.57, J. Kerr (NMV); 2 males, Murphy's Creek, SE Queensland, 30.ix.67, J.C. Cardale (UQIC); 1 male, Toowoomba, 24.viii.69, J.C. Cardale (UQIC); 2 females, 9 mi. W of Paluma, 3018 ft., 16.iv.69, I.F.B. Common and M.S. Upton (ANIC); 1 female, Paluma, viii.66, J.C. Cardale (UQIC); 2 females, Yuleba, 14.iv.69, T.F. Houston (UQIC); 2 females, Little Crystal Creek, Mt. Spec, 29.v.71, E.F. Riek (ANIC); 1 female, Collinsville, 15.ix.50, E.F. Riek (ANIC); 1 male, Bribie Is., 9.x.71, E.M. Exley (UQIC); 1 female, Ban-Ban Range via Coalstoun Lake, i.74, H. Frauca (ANIC); 3 females, 1 male, Bluff Range, Biggenden, 1-9.xii.71 - 9-20.xii.72, H. Frauca (ANIC); 2 females, 1 male, Mt. Walsh National Park via Biggenden, 9.i.73 - 17.i.77, H. Frauca (ANIC); 1 female, Coast Range near Biggenden, 22.xi.75, H. Frauca (ANIC); 1 female, Bundaberg, viii - ix.71, H. Frauca (ANIC); 1 female, Harvey Range, 29 mi. NW of Townsville, 1.xi.69, E.M. Exley (UQIC); 1 female, 11 mi. E of Howard, 10.viii.67, T.F. Houston (SAM); 1 female, Green Is., off Cairns, 21.viii.67, T.F. Houston (SAM); 1 female, Heifer Creek, SW of Gatton, 17.vi.67, T.F. Houston (SAM); 1 male, 2 mi. S of Nanango, 7.x.68, T.F. Houston (SAM); 1 male, 1 mi. W of Maidenwell, 9.x.68, T.F. Houston (SAM); 1 male, 3 mi. SW of Jimboomba, 25.i.68, T.F. Houston (SAM); 1 female, Eidsvold, x.29 - iv.30, T.L. Bancroft (ANIC); 2 females, 25° 9'S 151° 11'E, 24 km. N by E of Eidsvold, 11.x.84, I.D. Naumann and J.C. Cardale (ANIC); 1 female, 25° 34'S 149° 46'E, 8 km. NNW of Taroom, 9.x.84, I.D. Naumann and J.C. Cardale (ANIC); 1 female, 25° 25'S 149° 52'E, 26 km. N by E of Taroom, 9.x.84, I.D. Naumann and J.C. Cardale (ANIC); 1 female, 25° 10'S 149° 59'E, Isla Gorge National Park, 9.x.74, I.D. Naumann and J.C. Cardale (ANIC); 1 female, 25° 3'S 152° 14'E, 11 km. N by E of Cordalba, 9.ix.77, M.S. Upton and H. Frauca (ANIC); 1 female, 27° 39'S 150° 19'E, 9 km. NW by N of Moonie, 22.iv.81, I.D. Naumann (ANIC). **Northern Territory**. 1 male, 12° 52'S 132° 50'E, Koongarra, 15 km. E of Mt. Cahill, 15.xi.72, J.C. Cardale (ANIC); 9 females, 12° 52'S 132° 47'E, Nourlangie Creek, 8 km. E of Mt. Cahill, 17-18.xi.72, J.C. Cardale (ANIC); 2 females, 12° 48'S 132° 42'E, Nourlangie Creek, 8 km. N of Mt. Cahill, 16-17.vi.73, J.C. Cardale (ANIC); 1 female, 12° 50'S 132° 52'E, 19 km. E by N of Mt. Cahill, 18.xi.72, J.C. Cardale (ANIC); 1 female, 12° 23'S 132° 56'E, 7 km. NW by N of Cahills Crossing (E. Alligator River), 12-13.xi.72, J.C. Cardale (ANIC); 3 females, 12° 40'S 132° 54'E, Magela Creek, 9 km. SSE of Mudginbarry HS., 7-8.xi.72, J.C. Cardale (ANIC); 1 female, 12° 35'S 132° 52'E, Magela Creek, 2 km. N of Mudginbarry HS., 14-15.xi.72, J.C. Cardale (ANIC); 3 females, 12° 28'S 132° 52'E, Jabaluka (=Jabiluka) Lagoon, 14 km. N of Mudginbarry HS., 14.xi.72, J.C. Cardale (ANIC); 2 females, 12° 43'S 132° 54'E, Mt. Brockman, 14 km. S by E of Mudginbarry HS., 11-12.vi.73, J.C. Cardale (ANIC); 1 female, 12° 22'S 133° 1'E, 6 km. SW by S of Oenpelli, 6.vi.73, J.C. Cardale (ANIC); 1 female, 12° 65'S 133° 4'E, Cooper Creek, 19 km. E by S of Mt. Borradaile, 5-6.vi.73, J.C. Cardale (ANIC); 3 females, 5 males, 12° 17'S 133° 20'E, Cooper Creek, 11 km. S by W of Nimbuwah Rock, 3-4.vi.73, J.C. Cardale (ANIC); 1 female, 12° 18'S 133° 1'E, 15 km. SW by S of Nimbuwah Rock, 11-12.xi.72, J.C. Cardale (ANIC); 3 females, Arnhem, Maningrada, 5 m., 17-20.iii.61, J.L. Gressitt (Bishop); 1 female, Dreaming Waters, Woolwonga Fauna reserve, 20.x.73, E.F. Riek (ANIC); 1 male, 15° 58'S 136° 21'E, 12 km. NNE of Borroloola, 1.xi.75, J.C. Cardale (ANIC); 2 males, 129 mi. S of Darwin, 13.iii.73, E.M. Exley (UQIC); 3 males, 25 mi. N of Katherine, 16.iii.73, E.M. Exley (UQIC). **Western Australia**. 1 female, 1 male, 14° 40'S 125° 44'E, Surveyors Pool, 15.v.83, I.D. Naumann and J.C. Cardale (ANIC); 1 female, Merredin, 20.i.62, G.F. Mees (WAM); 1 female, 70-75 km. ENE of Norseman, 10-16.xi.78, T.F. Houston *et al.* (WAM). **New South Wales**. 1 female, Mt. Kaputar, 2000 ft., 5.ix.62, C.W. Frazier (ANIC); 1 female, Como, 4.ix.39 (ANIC); 1 female, 33 km. E of Narrabri, 2.xii.76, E.M. Exley and T. Low (UQIC); 3 males, 4 mi. NNE of Coonabarabran, 27.x.68, T.F. Houston (SAM); 1 male, Hawkesbury River, 29.x.30, A.N. Burns (NMV). **Victoria**. 3 females, Strathmore, 5.i.58, Spurell (NMV). **South Australia**. 11 females, Orroroo, 2.viii.41 (ANIC); 1 female, 33° 3'S 137° 9'E, North Middleback Range, 7-8.x.73, T.F. Houston; 1 female, Aroona HS. ruins, Flinders Range, North Park, 3.i.78, T.F. Houston (SAM).

Remarks. This species is similar in appearance to *B. minor* but can be separated from it by having the head broader than long and the pronotal lobe yellow. It is closely related to *B. nitida* and separated from it mainly on size. Plotting the head width measurements of both species shows a bimodal distribution (Fig. 6). It may be that *B. unicolor* and *B. nitida* are one species as there are no distinct characters that really separate these two species except size and size-related characters, i.e., scape length and form of the basitibial carina. However, I find it best at this time to conserve the specific rank of both species so that the locality information can be easily available if future studies are done to test the validity of the present hypothesis that these are indeed two separate species.

Most females from Northern Territory which have transparent tegulae have relatively thicker, curving and spiculate hairs on T4-6. These conditions grade into the usual features of slender hairs and dark tegulae from Queensland.

Braunsapis nitida (Smith)

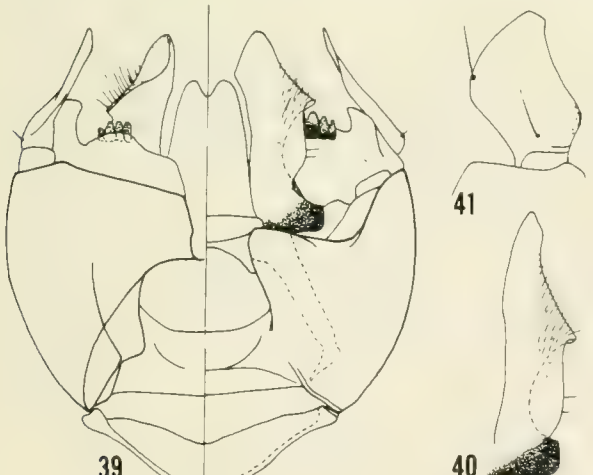
Allodape nitida Smith, 1858, p. 134. Type: female, Aru Island (Oxford).
Allodapula nitida Smith: Michener and Syed, 1962, pp. 34, 39; Michener, 1965, p. 233.

Female. Face as in Fig. 72. (1) Length 3.8 - 6.0 mm. (3) Lower half of clypeus partly black, clypeal mark narrow, strongly tapering towards apex. (6) Tegula transparent, translucent fuscous or dark, axillary sclerites yellow or mixed. (7) HW 1.16 - 1.53 mm. (8) HW/HL ratio 1.04 - 1.09. (11) Scape not reaching front ocellus. (12) Basitibial plate with carina weak. (13) Hairs on T4-6 black; longer hairs slanting, simple to blunt, equal to or slightly longer than width of scape; shorter hairs subprostrate, simple.

Male. Face as in Fig. 73. (14) Length 3.70 - 5.20 mm. (16) Clypeus yellow, clypeal mark narrow at base, broader on apical half. (18) HW 1.23 - 1.50 mm. (19) HW/HL ratio 1.11 - 1.15. (21) Hairs on T4-6 fuscous to black; longer hairs suberect, simple, longer than width of scape; shorter hairs subprostrate, simple. (22) Genitalia (n=8) as in Figs. 39-41; gonostylus with short seta medially, sometimes seta present on dorso-lateral margin (Fig. 41); ventro-apical plate of gonocoxite either symmetrical or asymmetrical, with 2-4 peg-like processes; penis valve slender, dorso-lateral gap wider than mid-lateral flange (Fig. 40).

Specimens examined. Type as listed. **New Guinea**. 56 males, Port Moresby, Papua, 25.iv.59, C.D. Michener (Bishop); 1 female, 25 mi. radius of Port Moresby, Papua, vi.28, Pemberton (Bishop); 1 female, Bisianumu, E of Port Moresby, 3.ix.59, T.C. Maa (Bishop); 1 female, Bulolo, 285 m., 24.viii.56, E.J. Ford (Bishop). **Queensland**. 5 females, Prince of Wales Is., Torres Strait, 14.ii.39, B.G. Wind (CAS); 2 females, Prince of Wales Is., Torres Strait, 27-30.v.69, Neboiss (NMV); 1 female, Banks Is., Torres Strait, 31.vi.69, Neboiss (NMV); 1 male, 5 km. WSW of St Pauls, Moa (Banks) Is., Torres Strait, 16.vii.77, G. Monteith and D. Cook (UQIC); 15 females, 12 males, 10° 12'S 142° 49'E, Warraber (Sue) Is., 2-10.xii.77, E.D. Edwards (ANIC); 2 females, Iron Range, Cape York Peninsula, 27.iv. - 4.v.73, S.R. Monteith (ANIC); 2 females, 11° 41'S 142° 45'E, Dividing Range, 15 km. N of Capt. Billy Creek, Cape York Peninsula, 4-9.vii.75, S.R. Monteith (ANIC); 2 males, 12° 43'S 143° 18'E, 11 km. ENE of Mt. Tozer, 11-16.vii.86, J.C. Cardale (ANIC); 1 male, Ellis Beach, 3.vii.66, K.R. Norris (ANIC); 4 females, Ellis Beach, N of Cairns, 21.iv.67, D.H. Colless (ANIC); 2 females, Somerset, 16-17.iv.73, S.R. Monteith (ANIC); 2 males, Cape Pallarenda, 19.viii.66, J.C. Cardale (UQIC); 2 females, Mossman, 11.xi.39 (ANIC); 1 female, 1 male, Edungalba, 28.iv. - 15.vii.40 (ANIC); 1 female, 15° 3'S 145° 15'E, 4 km. SW of Casuarina Hill, 30.iv. - 2.v.81, I.D. Naumann (ANIC); 1 female, 15° 3'S 145° 9'E, 3 km. NE of Mt. Webb, 1-30.x.80, J.C. Cardale (ANIC); 1 male, 15° 6'S 145° 14'E, 12-14 km. ESE of Mt. Webb, 3.x.80, J.C. Cardale (ANIC); 2 females, 15° 17'S 145° 10'E, 7 km. ENE of Hope Vale Mission, 5.x.80, J.C. Cardale (ANIC); 1 female, 15° 41'S 145° 12'E, Annan River, 3 km. W by S of Black Mt., 27.ix.80, J.C. Cardale (ANIC); 1 male, 26 mi. W of Mt. Garnet, 26.v.75, R.I. Storey (UQIC); 7 females, 25° 34'S 149° 46'E, 8 km. NNW of Taroom, 9.x.84, I.D. Naumann and J.C. Cardale (ANIC); 2 females, 25° 9'S 151° 11'E, 24 km. N by E of Eidsvold, 11.x.84, I.D. Naumann and J.C. Cardale (ANIC); 1 female, 28 km. NW of Mundubbera, 11.iii.76, E.M. Exley (UQIC); 1 female, 1 male, Morven, 3.xi.71, E.M. Exley (UQIC); 2 females, Moggill, Brisbane (nest no. 44), 27.ix.58, C.D. Michener (SMUK); 1 female, Brisbane, 26.xii.58, C.D. Michener (SMUK); 1 male, 13 mi. SE of Bowen, 13.viii.67, T.F. Houston (SAM); 1 female, 25 mi. NW of Bowen, 1.x.50, E.F. Riek (SMUK); 1 female, 8 km. W of Cunnamulla, 16.viii.66, E.M. Exley (UQIC); 1 female, Gordonvale, 19.viii.66, J.C. Cardale (UQIC); 1 male, 6 mi. W of Chinchilla, 14.iv.69, T.F. Houston (UQIC); 2 females, Mackay (BMNH); 1 female, Mackay (NMNH); 1 female, 1 male, Thursday Is. (NMNH); 1 male, 30 mi. N of Miles, 30.ix.67, T.F. Houston (SAM); 1 male, 3 mi. E of Mungallala, 29.ix.67, T.F. Houston (SAM). **Northern Territory**. 16 females, 1 male, Smith Point, Cobourg Peninsula, 10.ii.77, R.C. Lewis (ANIC); 1 female, 11° 9'S 132° 11'E, 7 km. ESE of Smith Point, Cobourg Peninsula, 23.i.77, E.D. Edwards (ANIC); 1 female, 11° 9'S 132° 9'E, Black Point, Cobourg Peninsula, 15-23.ii.77, T.A. Weir (ANIC); 18 females, 6 males, 11° 9'S 132° 9'E, Black Point, Cobourg Peninsula, 29-31.i.77, E.D. Edwards (ANIC); 1 male, 11° 1'S 136° 45'E, Rimbija Is., Wessel Is., 20.i.77, E.D. Edwards (ANIC); 2 females, 12° 17'S 133° 20'E, Cooper Creek, 11 km. S by W of Nimbuwah Rock, 3-4.vi.73, J.C. Cardale (ANIC); 39 females, 3 males, 12° 18'S 133° 17'E, 15 km. SW by S of Nimbuwah Rock, 10-11.xi.72, J.C. Cardale (ANIC); 3 females, 12° 25'S 132° 58'E, 1 km. NE of Cahills Crossing (E. Alligator River), 8-12.xi.72, J.C. Cardale (ANIC); 12 females, 12° 50'S 132° 52'E, 19 km. E of Mt. Cahill, 18.xi.72, J.C. Cardale (ANIC); 5 females, 1 male, 12° 48'S 132°42'E, Nourlangie Creek, 8 km. N of Mt. Cahill, J.C. Cardale (ANIC); 1 female, 12° 17'S 133° 13'E, Birraduk Creek, 18 km. E by N of Oenpelli, 4-5.vi.73, J.C. Cardale (ANIC); 1 female, 12° 31'S 132° 54'E, 9 km. N by E of Mudginbarry HS., 10-11.vi.73, J.C. Cardale (ANIC); 1 female, 1 male, 12° 28'S 132° 52'E, Jabaluka (=Jabiluka) Lagoon, 14 km. N of Mudginbarry HS., 14.xi.72, J.C. Cardale (ANIC); 2 males, Darwin, 12.iii.28, T.D.A. Cockerell (NMNH); 1 female, 1 male, Darwin, 10.iii.73, E.M. Exley (UQIC); 16 females, 2 males, Darwin, 2-4.xii.88, R.R. Snelling and J. Grey (LNHM); 1 female, Elizabeth River, 21 mi. S of Darwin, 28.x.70, T. Weir (UQIC); 1 male, 4 mi. of Marrakai, 13.ix.33, T.G. Campbell (ANIC); 1 female, 2 males, Arnhem Land, Maningrida, 5 m., 16-21.iii.61, J.L. and M. Gressitt (Bishop); 1 male, 16° 3'S 136° 19'E, 3 km. N by E of Borroloola, 31.x.75, J.C. Cardale (ANIC); 1 male, 16° 16'S 136° 5'E, Carumbirini Waterhole, 33 km. SW of Borroloola, 22.iv.66, J.C. Cardale (ANIC). **Western Australia**. 5 females, 14° 34'S 125° 50'E, 1 km. W of Walsh Point, 18.v.83, I.D. Naumann and J.C. Cardale (ANIC); 1 female, 14° 40'S 125° 44'E, Surveyors Pool, 15.v.83, I.D. Naumann and J.C. Cardale (ANIC); 1 female, 25° 15'S 122° 2'E, 37 km. SW of Glenayle HS., 8-9.viii.83, T.F. Houston and R.P. McMillan (WAM); 2 females, 22° 38'S 118° 6'E, Marandoo Camp, 5-19.v.80, T.F. Houston *et al.* (WAM); 1 female, 30° 59'S 119° 7'E, Mt. Jackson, 5-11.ix.79, T.F. Houston *et al.* (WAM). **New South Wales**. 1 female, 30.ix.76, 34 km. SE of Moree, E.M. Exley and T. Low (UQIC). **South Australia**. 2 females, Orroroo, 2.viii.41 (ANIC); 1 male, 33° 3'S 137° 9'E, North Middleback Range, 7-8.x.73, C.A. and T.F. Houston (SAM).

Remarks. Three females from Western Australia and three from Northern Territory have the clypeal mark hour-glass shaped and usually with yellow marks on the labrum. Variation in tegular color in the species is shown in Fig. 5.



Figs. 39-41. Male genitalia of *B. nitida*, Warraber (Sue) Is., Queensland. **Fig. 39.** Dorsal (right) and ventral (left) view of genitalia. **Fig. 40.** Penis valve, dorso-apical view. **Fig. 41.** Gonostylus, lateral view.

Braunsapis biroi (Friese)

Allodape biroi Friese, 1909, p. 209. Types: 7 females and 1 male, Simbang and Sattelberg, New Guinea, Biró (Budapest).
Allodapula nitida Smith: Michener, 1965, p. 233.

Lectotype: female, Sattelberg, New Guinea, Biró (Budapest), hereby designated. *Paralectotypes*: 3 females, same data except 1 female deposited in SMUK; 1 female, same data except Simbang, New Guinea.

Female. Face as in Figs. 74-75. (1) Length 3.8 - 4.4 mm. (2) Labrum and mandible ferrugino-testaceous to slightly fuscous. (3) Lower half of clypeus partly black, clypeal mark narrow, tapering strongly towards the apex. (4) Paraocular area with elongate mark. (6) Tegula transparent, axillary sclerites yellow. (7) HW 1.13 - 1.16 mm. (8) HW/HL ratio 1.04 - 1.09. (10) Middle of epistomal suture almost flat. (11) Scape not reaching front ocellus. (12) Basitibial plate with carina weak. (*) Second recurrent vein entering second marginal cell two thirds length of cell from base or less (Fig. 4). (13) Hairs on T4-6 black; longer hairs suberect, simple, longer than width of scape; shorter hairs subprostrate to prostrate, simple.

Specimens examined. **New Guinea**. 21 females, Sattelberg, 1899, Biró (Budapest); 3 females, same data except (SMUK); 4 females, Simbang, 1899, Biró (Budapest); 1 female, same data except (SMUK). **Queensland**. 4 females, Iron Range, Cape York Peninsula, N. Queensland, 28.iv.68 - 11-17.v.68, G. Monteith (UQIC).

Remarks. This species is readily distinguished from all others by having the second recurrent vein entering the second marginal cell one-third of the length of that cell from its apex (Fig. 4). The type could not be located and is presumed lost. I received a series of six females with Friese's determination label and collected from the same localities (Sattelberg and Simbang, New Guinea) listed for the species by Friese and I assume these are syntypes. One female belongs to the genus *Homalictus* (Halictidae) and the other five specimens fit the description. Friese (1909), however, failed to note the presence of small paraocular marks in most of the specimens (3 out of 5 from the syntypes; 20 out of 29 additional specimens from the same localities as the type series). The designated lectotype conforms to Friese's description and lacks the paraocular marks.

THE *ASSOCIATA* SPECIES GROUP

The females of the *associata* species group have the tip of the last metasomal tergum scoop-shaped (Figs. 92, 93). Michener (1961) collected *B. platyura* (=*associata* Michener, 1961, in part) from the nest of *B. unicolor* and suggested that this species and *B. praesumptiosa* might be social parasites of other *Braunsapis* species (Michener, 1961, 1970, 1974). Specimens of this group have been collected on flowers, however, and except for the modified apex of abdomen they do not exhibit morphological features associated with parasitic behavior. Some female specimens of all six species recognized in this paper have abundant pollen on their scopae. This indicates that these bees do collect pollen and probably are not parasitic. Occupation of a nest by two different species could have been the result of some environmental stress (e.g., lack of favorable nesting sites), not necessarily parasitism (Reyes and Michener, 1990). Nest sharing by related species in the pre-reproductive assemblage stage has been observed for *Exoneura* (Michener, personal communication). Since Michener's collection was made in spring (1958), it likely contained bees still in pre-reproductive assemblages. The reduction of the basitibial plate is also a feature associated with parasitism; the carina which defines the posterior margin of the basitibial plate is weak or absent in parasitic species (Michener, 1961, 1966). The basitibial plate is not well developed in allodapines, and the development of the carina is correlated with the size of the individual, being generally weak or indistinct in smaller specimens and species and usually raised in larger ones (Table 1); it is not unusually reduced in the *associata* group.

Each species of this group closely resembles a species in the *diminuta* or *simillima* species groups. Moreover, the males of the *associata* group are unknown in spite of numerous females; probably males have not been distinguished from those of similar species. These facts could be interpreted as meaning that each species of a monophyletic *associata* group has converged towards a species (probable host ?) in another group. A more likely explanation is that the scoop-shaped abdomen has evolved six times in different *Braunsapis* species. Finally, a possible explanation is that, in spite of the major morphological differences between the females of the *associata* group and those of related species groups, some species of the *diminuta* and *simillima* species groups vary in the form of the metasomal apex. Species with similar scoop-shaped metasomal apices (a probable or clearly specific character) occur in the African *B. paradoxa* and *vitrea* species groups, in the Asiatic *B. breviceps* (Cockerell) which is unquestionably parasitic, as well as in some species of the related genera *Allodape* and *Exoneurella.*

Braunsapis associata (Michener)

Allodapula associata Michener, 1961, p. 533 (holotype only). Type: female, Mt. Edwards, S. Queensland, 29.ix.58, C.D. Michener (QM); Michener and Syed, 1962, p. 41; Michener, 1965, p. 233.

Female. Face as in Fig. 76. (1) Length 5.5 - 7.5 mm. (2) Labrum and mandible black. (3) Lower half of clypeus partly black. (4) Paraocular mark absent. (5) Pronotal lobe yellow. (6) Tegula translucent fuscous, axillary sclerites yellow. (7) HW 1.66 - 1.90 mm. (8) HW/HL ratio 1.08 - 1.10. (9) Malar space shorter than width of scape. (10) Middle of epistomal suture slightly raised. (11) Scape reaching front ocellus. (12) Basitibial plate with raised carina, sometimes weak. (13) Hairs on T4-6 fuscous; longer hairs suberect, simple to blunt, almost as long as width of scape; shorter hairs subprostrate, simple. (*) T6 scoop-shaped, tip pointed and strongly curved upwards in lateral view (Fig. 92).

Specimens examined. Type as listed. **Queensland**. 1 female, Prince of Wales Is., 14.ii.39, R.G. Wind (CAS); 1 female, Mt. Nebo, 23.ii.67, J. Kerr (UQIC); 1 female, 14 mi. ESE of Marlborough, 11.viii.67, T.F. Houston (SAM); 1 female, Normanby River Crossing, 19.viii.67, T.F. Houston (SAM); 1 female, Bluff Range Biggenden, 1-19.xii.71, H. Frauca (ANIC); 1 female, Lockerbie Area, Cape York, 13-27.iv.73, S.R. Monteith (ANIC). **Northern Territory**. 4 females, 12° 48'S 132° 42'E, Nourlangie Creek, 8 km. N of Mt. Cahill, 16-17.vi.73, J.C. Cardale (ANIC); 1 female, 12° 50'S 132° 52'E, 19 km. E by N of Mt. Cahill, 14.vi.73, J.C. Cardale (ANIC); 1 female, 12° 22'S 132° 52'E, 6 km. SW by S of Oenpelli, 6.vi.73, J.C. Cardale (ANIC); 1 female, 12° 18'S 133° 17'E, 15 km. SW by S of Nimbuwah Rock, 10-11.xi.72, J.C. Cardale (ANIC).

Remarks. B. associata closely resembles *B. simillima* but can be readily separated from it by its scoop-shaped T6. It also differs from *B. praesumptiosa* by having the tip of T6 pointed and curved upward in lateral view (Fig. 92). In addition, the tegula is translucent fuscous and the axillary sclerites are yellow while those of *B. praesumptiosa* are fuscous to black.

Five females, one from Queensland and four from Northern Territory, have the hairs on T4-5 simple and over twice as long as the width of the scape. The clypeal mark is also somewhat narrower at the base in these specimens than *B. praesumptiosa.*

Braunsapis praesumptiosa (Michener)

Allodapula praesumptiosa Michener, 1961, p. 533. Type: female, Mackay, Queensland, iv.1899 (BMNH); Michener and Syed, 1962, p. 41; Michener, 1965, p. 233.

Female. Face as in Fig. 77. (1) Length 1.63-2.23 mm. (3) Lower half of clypeus partly black, clypeal mark narrow, strongly tapering toward apex. (6) Tegula and axillary sclerites fuscous to black. (7) HW 1.63-2.23 mm. (8) HW/HL ratio 1.08 - 1.11. (10) Middle of epistomal suture raised. (12) Basitibial plate with carina raised or conical, sometimes weak or indistinct. (13) Hairs on T4-6 fuscous to black; longer hairs suberect, simple, about 2-3 times as long as width of scape; shorter hairs subprostrate, simple. (*) T6 scoop-shaped, blunt at tip, slightly curved in lateral view (Fig. 93).

Specimens examined. Type as listed. **Queensland**. 2 females, Prince of Wales Is., 14.ii.39, R.G. Wind (CAS); 8 females (paratypes), Mackay (BMNH); 1 female (paratype), Mackay (ANIC); 7 females, Bluff Range, nr. Biggenden, 17-19.viii.71-3-16.x.74, H. Frauca (ANIC); 1 female, Murphy Creek, SE Queensland, 30.ix.67, J.C. Cardale (UQIC); 1 female, Mt. Walsh Nat. Park via Biggenden, 22.viii.72, H. Frauca (ANIC); 1 female, Rockpool Gorge, Mt. Walsh Nat. Park, Bluff Range, Biggenden, 29.i.76, H. Frauca (ANIC); 1 female, Kuranda, 1916-27 (NMNH); 2 females, Cooktown, 14.xi.78, E.M. Exley and K. Walker (UQIC); 1 female, 6 mi. SW of Warwick, 17.x.71, E.M. Exley (UQIC); 1 female, Maryborough, 30.viii.66, J.C. Cardale (UQIC); 1 female, Mt. May via Boonah, 10.x.65, J.C. Cardale (UQIC); 1 female, S of Beerwah, 2.x.66, J.C. Cardale (UQIC); 3 females, Mt. Nebo, 23.ii.57, J. Kerr (UQIC); 1 female, Stradbroke Island, 17.ix.15, H. Hacker (QM); 1 female, sandstone outcrop 30 km. W of Fairview via Laura, 22-24.vi.76, G.B. and S.R. Monteith (ANIC); 1 female, Nerang, 22.i.68, T.F. Houston (SAM); 2 females, Tibrogargan Creek, 12.viii.66, T.F. Houston (SAM); 1 female, Shute Harbour, 13.viii.67 (SAM); 1 female, 16 mi. from Fernvale, 19.xii.66, J.C. Cardale (UQIC); 1 female, 15° 3'S 145 15'E 4 km. SW of Casuarina Hill, 30.iv-2.v.81, I.D. Naumann (ANIC).

Remarks. This species resembles *B. protuberans* except that the middle of the epistomal suture is not conically raised and T6 is scoop-shaped. The scoop-shaped end of T6 is not strongly curved upward in profile like that of *B. associata*, *B. eximia*, and *B. falcata*. The hair form of T4-5 of this species is similar to that of *B. clarissima* but the hairs are fuscous to black.

Braunsapis eximia, n. sp.

Holotype: female, 11° 9'S 132° 9'E, Black Point, Cobourg Peninsula, Northern Territory, 31.i.77, E.D. Edwards (ANIC). *Paratypes*: **Northern Territory**. 4 females same data as holotype; 4 females, 12° 18'S 133° 17'E, 15 km. SW by S of Nimbuwah Rock, 10-11.xi.72, J.C. Cardale (ANIC); 1 female, 12° 48'S 132° 42'E Nourlangie Creek, 8 km. N of Mt. Cahill, 19-20.xi.72, J.C. Cardale (ANIC); 1 female, 12° 50'S 132° 52'E 19 km. E by N of Mt. Cahill, 14.vi.73, J.C. Cardale (ANIC).

Female. Face as in Fig. 78. (1) Length 4.2 - 5.4 mm. (3) Lower half of clypeus partly black, clypeal mark narrow, strongly tapering toward apex, sometimes not reaching apex. (6) Tegula translucent fuscous, axillary sclerites yellow. (7) HW 1.20 - 1.43 mm (1.40 mm). (8) HW/HL ratio 1.04 - 1.05. (12) Basitibial plate with carina indistinct. (13) Hairs on T4-5 fuscous to black; longer hairs suberect, simple, longer than width of scape; shorter hairs subprostrate, simple. (*) T6 as in *B. associata*.

Remarks. This species is similar in general appearance to *B. nitida* but differs from it by having the basitibial plate indistinct and T6 scoop-shaped. It can be separated from *B. falcata* by the dark hairs on T4-5 and by the narrow and strongly tapering clypeal mark (Fig. 78).

The specific name *eximia* is derived from the Latin *eximius*, meaning extraordinary, with reference to the scoop-shaped T6.

Braunsapis falcata, n. sp.

Allodapula associata Michener, 1961, p. 533 (in part).

Holotype: female, Derby, Western Australia, 26.ii.73, E.M. Exley (QM). *Paratypes*: **Western Australia**. 5 females, same data as holotype (UQIC); 3 females, Broome, 28.ii.73, E.M. Exley (UQIC); 1 female, Broome, 14.ii.75, E. Exley and R. Storey (UQIC); 5 females, 14° 40'S 125° 44'E, Surveyors Pool, 15.v.83, I.D. Naumann and J.C. Cardale (ANIC); 1 female, 15° 2'S 126° 55'E, Drysdale River, 3-8.viii.75, I.F.B. Common and M.S. Upton (ANIC); 1 female, 15° 2'S 126° 40'E, Morgan Falls, 16-17.viii.75, I.F.B. Common and M.S. Upton (ANIC). **Northern Territory**. 1 female, Darwin, Turner Coll. (BMNH); 2 females, 15 mi. E and 25 mi. N of Katherine, 15-16.iii.63, E.M. Exley (UQIC); 2 females, 15° 58'S 136° 21'E, 12 km. NNE of Borroloola, 1.xi.75, J.C. Cardale (ANIC); 1 female, 16° 8'S 136° 6'E, 22 km. WSW of Borroloola, 2.xi.75, J.C. Cardale (ANIC); 2 females, 19 km. N of Daly Waters, 16.xi.74, E.M. Exley and R.I. Storey (UQIC); 1 female, 8 km. N of Mataranka, 19.xi.74, E.M. Exley and R.I. Storey (UQIC); 1 female, 17 km. along Mt. Bundey Rd. via Darwin, 24.xi.74, E.M. Exley and R.I. Storey (UQIC); 1 female, 12 km. SW of Katherine, 21.xi.74, E.M. Exley and R.I. Storey (UQIC); 1 female, 15° 54'S 136° 32'E, Batten Point, 30 km. NE by E of Borroloola, 30.x.75, J.C. Cardale (ANIC); 1 female, 12° 6'S 133° 20'E, Cooper Creek, 11 km. S by W of Nimbuwah Rock, 3-4.vi.73, J.C. Cardale (ANIC); 2 females, 12° 6'S 133° 4'E, Cooper Creek, 19 km. E by S of Mt. Borradaile, 5-6.vi.73, J.C. Cardale (ANIC); 1 female, 12° 43'S 132° 54'E, Mt. Brockman, 14 km. S by E of Mudginbarry HS., 11-12.vi.73, J.C. Cardale (ANIC); 1 female, Darwin, G.F. Hill (AM). **Queensland**. 1 female, Prince of Wales Is., 14.ii.39, R.G. Wind (CAS); 1 female, same data except (SMUK); 1 female, 13 mi. W of Georgetown, 260 m., 4.xi.62, E.S. Ross and D. Cavagnaro (CAS); 1 female, Mackay, iii.00 (=paratype of *associata* of Michener, 1961) (BMNH); 1 female, Mt. Isa, 3.xi.67, E.M. Exley (UQIC).

Female. Face as in Fig. 79. (1) Length 4.5 - 6.0 mm. (6) Tegula transparent, axillary sclerites yellow. (7) HW 1.27 - 1.66 mm (1.36 mm). (8) HW/HL ratio 1.02 - 1.03. (12) Basitibial plate with carina weak to indistinct. (13) Hairs on T4-5 transparent; longer hairs suberect, blunt to spiculate, slightly longer than width of scape; shorter hairs subprostrate, simple. (*) T6 as in *B. associata*.

Remarks. This species is found mainly in Western Australia and Northern Territory, but five specimens are from Queensland. It is quite simlar in appearance to *B. diminuta* except for the scoop-shaped T6 and somewhat narrower head (HW/HL ratio 1.02 - 1.03).

The specific name *falcata* is derived from the Latin *falcatus*, meaning curved like a sickle, referring to the tip of T6 which is pointed and curved upward as seen in profile.

Braunsapis platyura, n. sp.

Allodapula associata Michener, 1961, p. 533 (in part).

Holotype: female, 25° 34'S 149° 46'E, 8 km. NNW of Taroom, Queensland, 9.x.84, I.D. Naumann and J.C. Cardale (ANIC). *Paratypes*: **Queensland**. 8 females, Prince of Wales Is., Cape York, J.A. Kusche (Bishop); 1 female, 2-4 mi. from Fernvale, 19.xii.66, J.C. Cardale (UQIC); 1 female, Mungallala, 3.xi.71, E.M. Exley (UQIC); 1 female, Murphy Creek, SE Queensland, 30.ix.67, J.C. Cardale (UQIC); 1 female, Eidsvold, 8.ix.29 (=paratype of *associata* of Michener, 1961) (ANIC); 1 female, Yaamba, 11.viii.58, C.D. Michener (=paratype of *associata* of Michener, 1961, nest no. 39) (SMUK); 3 females, Wandoo Sta., 10.viii.58, C.D. Michener (=paratypes of *associata* of Michener, 1961, nest nos. 17, 58) (SMUK).

Female. Face as in Fig. 80. (1) Length 5.0 - 7.5 mm. (6) Tegula translucent fuscous, axillary sclerites yellow, sometimes mixed. (7) HW 1.37 - 1.70 mm (1.37 mm). (8) HW/HL ratio 1.03 - 1.04. (12) Basitibial plate with carina weak to indistinct. (13) Hairs on T4-5 transparent; longer hairs suberect, simple to blunt, longer than width of scape; shorter hairs subprostrate, simple. (*) T6 slightly scoop-shaped, almost flat, tip blunt.

Remarks. Five paratypes of *B. associata* are included in this species because they have the tip of the last metasomal tergum flat and blunt. These bees were collected together with *B. unicolor* (nest no. 39 examined) by C.D. Michener (1961) who suggested that these

are probably social parasites of the latter. Examination of several field-collected females showed that they had pollen on their scopae and it is likely that these are not really social parasites as Michener suggested. However, the real relationship between these two species still needs to be ascertained, as noted in the discussion under the *associata* species group. *B. platyura* closely resembles *B. diminutoides* in general appearance but differs from it by having a translucently fuscous tegula, the head narrower (HW/HL ratio 1.03 - 1.04) and T6 scoop-shaped.

The specific name *platyura* is from the Greek *platys*, meaning flat, plus *oura* meaning tail, referring to the almost flat and blunt tip of T6.

Braunsapis hirsuta, n. sp.

Allodapula associata Michener, 1961, p. 533 (in part).

Holotype: female, 12° 52'S 132° 50'E, Koongarra, 15 km. E of Mt. Cahill, Northern Territory, 12-13.vi.73, J.C. Cardale (ANIC). *Paratypes*: **Northern Territory**. 1 female, 12° 48'S 132° 42'E, Nourlangie Creek, 8 km. N of Mt. Cahill, 16-17.vi.73, J.C. Cardale (ANIC); 1 female, 16° 8'S 136° 6'E, 22 km. WSW of Borroloola, 2.xi.75, J.C. Cardale (ANIC); 1 female, 12° 43'S 132° 54'E, Mt. Brockman, 14 km. S by E of Mudginbarry HS., 11-12.vi.73, J.C. Cardale (ANIC); 1 female, 19 km. N of Daly Waters, 16.xi.74, E.M. Exley and R.I. Storey (UQIC). **Queensland**. 1 female, Mackay, iv.1899 (NMNH); 1 female, Yaamba, 11.viii.58, C.D. Michener (=paratype of *associata* of Michener, 1961) (SMUK); 1 female, Mareeba, 23.i.55, G.B. (=paratype of *associata* of Michener, 1961) (UQIC); 1 female, Glenmorgan, 22.x.58, C.D. Michener (Bishop); 1 female, Rockhampton, 12.vii.58, C.D. Michener (Bishop); 2 females, 28 mi. S of Palmer River, Cooktown H'way., 18.v.75, R.I. Storey (UQIC); 1 female, Townsville, 26.ii.02, F.P. Dodd (BMNH); 1 female, 16° 24'S 144° 47'E, Kelly St. George River, 14 km. W of Mt. Desailly, 26.iv.81, I.D. Naumann (ANIC); 1 female, sandstone outcrops 30 km. W of Fairview via Laura, 22-24.vi.76, G.B. and S.R. Monteith (ANIC); 1 female, 20 mi. N of Collinville, 2.v.68, T.F. Houston SAM); 1 female, Murphy Creek, SE Queensland, 30.ix.67, J.C. Cardale (UQIC).

Female. Face as in Fig. 81. (1) Length 6.10 -7.50 mm. (6) Tegula transparent, sometimes infuscated mesally, axillary sclerites yellow. (7) HW 1.63 - 1.90 mm (1.90 mm). (8) HW/HL ratio 1.06 - 1.08. (12) Basitibial plate with carina conically produced. (13) Hairs on T4-5 transparent; longer hairs suberect, simple, about twice as long as width of scape; shorter hairs subprostrate to prostrate, simple. (*) T6 as in *B. associata*.

Remarks. This species closely resembles *B. clarissima* but differs from it by having the head narrower (HW/HL ratio 1.06 - 1.08) and T6 scoop-shaped. The name *hirsuta* comes from the Latin *hirsutus*, meaning hairy, referring to the long transparent hairs on T4-5.

THE *MINOR* SPECIES GROUP

This group is distinguished by having the head longer than broad or as long as broad. The malar space is either longer than or about as long as the width of the scape, except shorter in *B. hyalina*. The females have either black or transparent hairs. The males are unknown except for *B. hyalina* and *dolichocephala* which have lobed hind trochanters.

Braunsapis occidentalis (Michener and Syed)

Allodapula occidentalis Michener and Syed, 1962, p. 41. Type: female, Tambrey, Western Australia, 2.viii.58, R.P. McMillan (WAM); Michener, 1965, p. 233.

Female. Face as in Fig. 82. (1) Length 5.5 - 6.5 mm. (2) Labrum and mandible black. (3) Lower half of clypeus partly black. (4) Paraocular mark absent. (5) Pronotal lobe yellow. (6) Tegula transparent, axillary sclerites yellow. (7) HW 1.63 - 1.80 mm. (8) Head about as long as wide. (9) Malar space about as long as width of scape. (10) Middle of epistomal suture slightly raised. (11) Scape reaching front ocellus. (12) Basitibial plate with carina conically raised. (13) Hairs on T4-6 transparent; longer hairs suberect, curved, spiculate apically, slightly longer than width of scape; shorter hairs prostrate, spiculate.

Specimens examined. Type as listed. **Northern Territory**. 1 female, 23° 40'S 134° 13'E, 5 km. SW of Corroboree Rock, 28.x.77, J.C. Cardale (ANIC).

Remarks. The specimen from Northern Territory has a yellowish mark on the underside of the scape. This species can be readily distinguished by having the head as long as broad and the malar space as wide as the width of scape.

Braunsapis minor (Michener and Syed)

Allodapula minor Michener and Syed, 1962, p. 38-39. Type: female, Mackay, Queensland, Turner Coll. (BMNH); Michener, 1965, p. 233.

Female. Face as in Fig. 83. (1) Length 4.5 - 5.0 mm. (3) Lower half of clypeus partly black, clypeal mark narrow, strongly tapering and sometimes not reaching apex. (5) Pronotal lobe black. (6) Tegula translucent fuscous, sometimes transparent along outer margin, axillary sclerites dark or partly yellow. (7) HW 1.16 - 1.20 mm. (8) HW/HL ratio 0.94 - 0.97. (9) Malar space slightly shorter than width of scape. (10) Middle of epistomal suture slightly raised. (11) Scape not reaching front ocellus. (12) Basitibial plate with weak carina. (13) Hairs on T4-6 black; longer hairs slanting, spiculate, about as long as width of scape; shorter hairs subprostrate, simple.

Specimens examined. Type as listed. **Queensland**. 2 females (paratypes), Mackay (BMNH).

Remarks. This species is easily separated by having its head longer than broad and the pronotal lobe black.

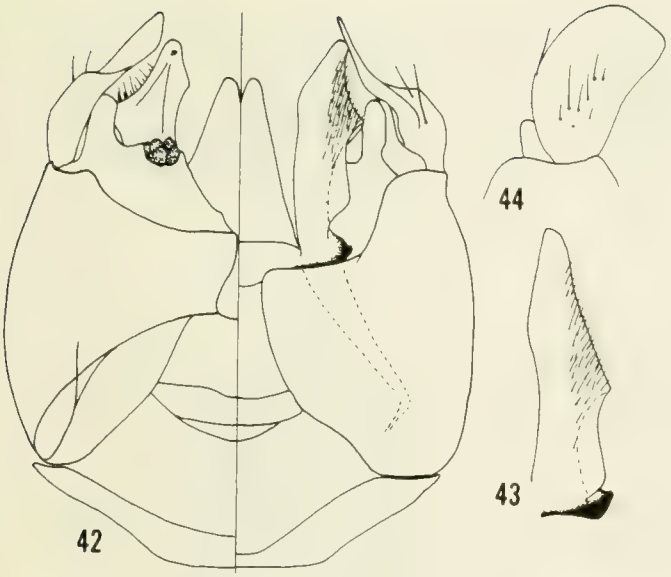
Braunsapis dolichocephala, n. sp.

Holotype: female, 24° 11'S 134° 1'E, 56 km. S by E of Alice Springs, Northern Territory, 3.x.78, J.C. Cardale (ANIC). *Paratypes*: 4 females, 1 male, Areyonga, 600 m., 8.viii-8.xii, Townes (AEI); 2 females, same data except (SMUK); 1 female, Yuendumu, 25.viii-14.ix, Townes (AIE).

Female. Face as in Fig. 84. (1) Length 6.4 - 7.5 mm. (2) Labrum dark reddish brown, mandible black. (*) Scape with yellowish mark on underside. (7) HW 1.70 - 1.90 mm (1.80 mm). (8) HW/HL ratio 0.93 - 0.94. (9) Malar space about twice the width of scape. (10) Middle of epistomal suture strongly raised. (12) Basitibial plate with carina weak. (13) Hairs on T4-6 transparent; longer hairs strongly bent, almost subprostrate, spiculate, about as long as width of scape; shorter hairs prostrate, spiculate.

Male. Face as in Fig. 85. (14) Length 5.8 mm. (15) Labrum yellow, mandible black. (16) Clypeus yellow. (17) Paraocualr mark present. (*) Scape yellow on under side. (18) HW 1.53 mm. (19) HW/HL ratio 0.92. (20) Trochanter excised medially and lobed distally. (21) Hairs on T4-6 transparent; longer hairs slanting, weakly spiculate, about as long as width of scape; shorter hairs prostrate, spiculate. (22) Genitalia as in Figs. 42-44; gonostylus with 7 setae medially, one seta dorso-laterally (Fig. 44); ventro-apical plate of gonocoxite symmetrical, with 5 peg-like processes; penis valve slender, dorso-lateral gap wider than mid-lateral flange (Fig. 43).

Remarks. This species is quite remarkable in having the malar space about twice as long as the width of the scape and the head noticably longer than broad. Hence, the name *dolichocephala* from the Greek *dolichos*, meaning long, plus *kephale*, meaning head.



Figs. 42-44. Male genitalia of *B. dolichocephala* (paratype), Areyonga, Northern Territory. **Fig. 42.** Dorsal (right) and ventral (left) view of genitalia. **Fig. 43.** Penis valve, dorso-apical view. **Fig. 44.** Gonostylus, lateral view.

Braunsapis hyalina, n. sp.

Holotype: female, 13 mi. W of Georgetown, 260 m, Queensland, 4.ix.62, E.S. Ross and D. Cavagnaro (CAS). *Paratypes*: 45 females, 3 males, same data as holotype; 3 females, 1 male, same data except (SMUK); 2 females, 1 male, same data except (ANIC).

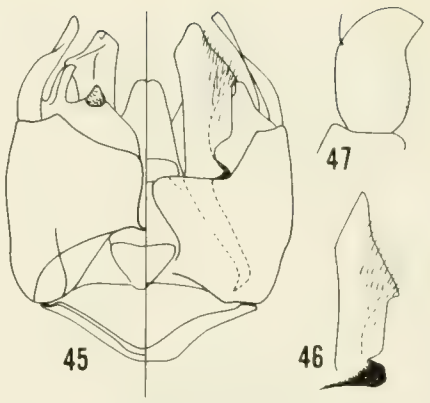
Female. Face as in Fig. 86. (1) Length 3.7 - 5.4 mm. (2) Labrum dark reddish brown, sometimes with yellow mark, mandible black. (4) Paraocular mark absent, rarely with pair of spots. (7) HW 1.07 - 1.50 mm (1.16 mm). (8) Head as long as broad. (9) Malar space shorter than width of scape. (10) Middle of epistomal suture raised. (11) Scape not reaching front ocellus. (12) Basitibial plate with carina weak. (13) Hairs on T4-6 transparent to light brown; longer hairs suberect, spiculate to slightly plumose at tip, longer than width of scape; shorter hairs subprostrate, slightly spiculate.

Male. Face as in Fig. 87. (14) Length 3.25 - 4.0 mm. (15) Labrum and mandible mainly yellow. (16) Clypeus yellow. (17) Paraocular mark present. (18) HW 1.10 - 1.17 mm. (19) HW/HL ratio 1.02 - 1.04. (20) Hind trochanter lobed with yellow spot posteriorly. (21) Hairs on T4-6 transparent to light brown; longer hairs suberect, simple, slightly longer than width of scape; shorter hairs subprostrate, simple. (22) Genitalia (n=2) as in Figs. 45-47; gonostylus with short seta medially, sometimes seta present dorso-laterally (Fig. 47); ventro-apical plate of gonocoxite symmetrical, with 1 peg-like process; penis valve with mid-lateral flange broad, dorso-lateral gap wider than mid-lateral flange (Fig. 46).

Additional specimens examined. Types as listed. **Queensland**. 7 females, same data as holotype; 2 females, same data except (SMUK); 1 female, Toowoomba, 500 m., 23.xi.62, E.S. Ross and D. Cavagnaro (CAS); 1 female, Mt. Isa and vicinity, 30-31.viii.72, H.E. Evans and R.W. Matthews (MCZ).

Remarks. This species can be confused easily with *B. diminuta* because of its size and having whitish or transparent hairs on T4-6. However, the head is more rounded, whereas in *diminuta* it is clearly broader than long. It differs from *B. minor* in having transparent hairs instead of black on T4-6. The five female specimens with small spots on the paraocular areas agree well with the rest of the characters and therefore are placed in this species.

The specific name *hyalina* is derived from the Latin *hyalinus*, meaning transparent, referring to the transparent hair on T4-6.



Figs. 45-47. Male genitalia of *B. hyalina* (paratype), 13 km. W of Georgetown, Queensland. **Fig. 45.** Dorsal (right) and ventral (left) view of genitalia.. **Fig. 46.** Penis valve, dorso-apical view. **Fig. 47.** Gonostylus, lateral view.

ACKNOWLEDGMENTS

I am especially grateful to Dr. Charles D. Michener and the anonymous reviewer for many helpful suggestions on the draft of the manuscript and to Lorraine Hammer, previously of the Division of Biological Sciences, University of Kansas, for her technical assistance in the use of the scanning electron microscope. This study was made possible thanks to the National Science Foundation Grant BSR 87-16817 (C.D. Michener, principal investigator).

To the institutions and persons listed under Materials and Methods, I am very grateful for the loan of the specimens. I am indebted to G. Else of the Natural History Museum, London, for help in locating the type of *B. biroi*.

LITERATURE CITED

Cardale, J. C. 1993. Hymenoptera: Apoidea *in* W. W. K. Houston and G. V. Maynard, eds., Zoological Catalogue of Australia, 10:ix + 405 pp., Canberra: AustralianGovernment Publishing Service.

Cockerell, T. D. A. 1915. Descriptions and records of bees. - LXV. Annals and Magazine of Natural History, ser. 8, 15:261-269.

———. 1929a. Bees from the Australian region. American Museum Novitates no. 346, pp. 1-18.

———. 1929b. Description and records of bees. - CXVIII. Annals and Magazine of Natural History, ser 10, 4:142-152.

Friese, H. 1909. Die Bienenfauna von Neu-Guinea. Ann. Mus. Nat. Hungarici 7:179-288.

Krombein, K. V. 1951. Additional notes on the bees of the Solomon Islands (Hymenoptera: Apoidea). Proceedings of the Hawaiian Entomological Society 14:277-295.

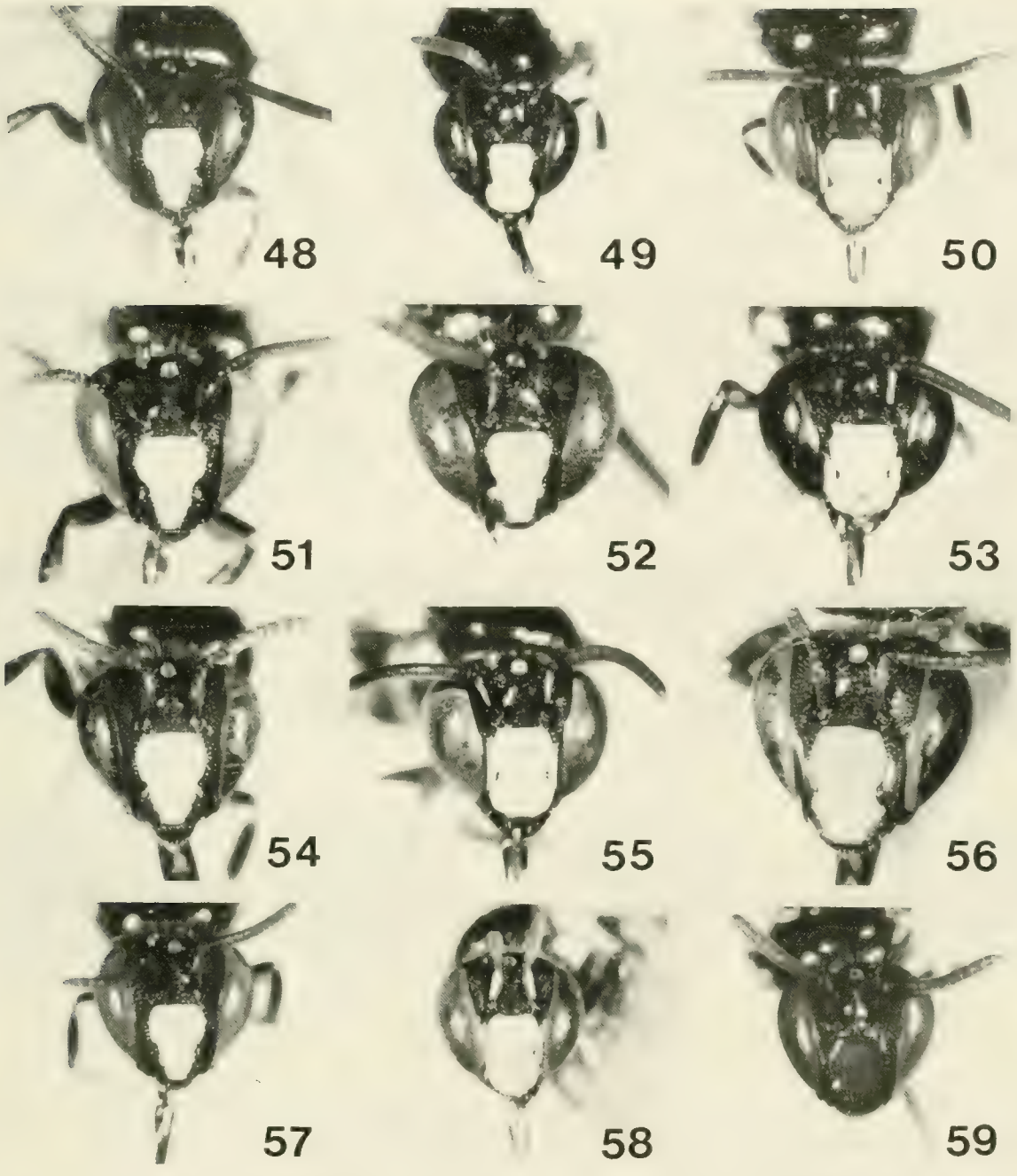
Maeta, Y., M. Shiokawa, S. F. Sakagami and C. D. Michener. 1984. Field studies in Taiwan on nesting behavior of a social xylocopine bee, *Braunsapis sauteriella*. Kontyû 52:266-277.

———, S. F. Sakagami and C. D. Michener. 1985. Laboratory studies on the life cycle and nesting biology of *Braunsapis sauteriella*, a social xylocopine bee (Hymenoptera: Apidae). Sociobiology 10:18-42.

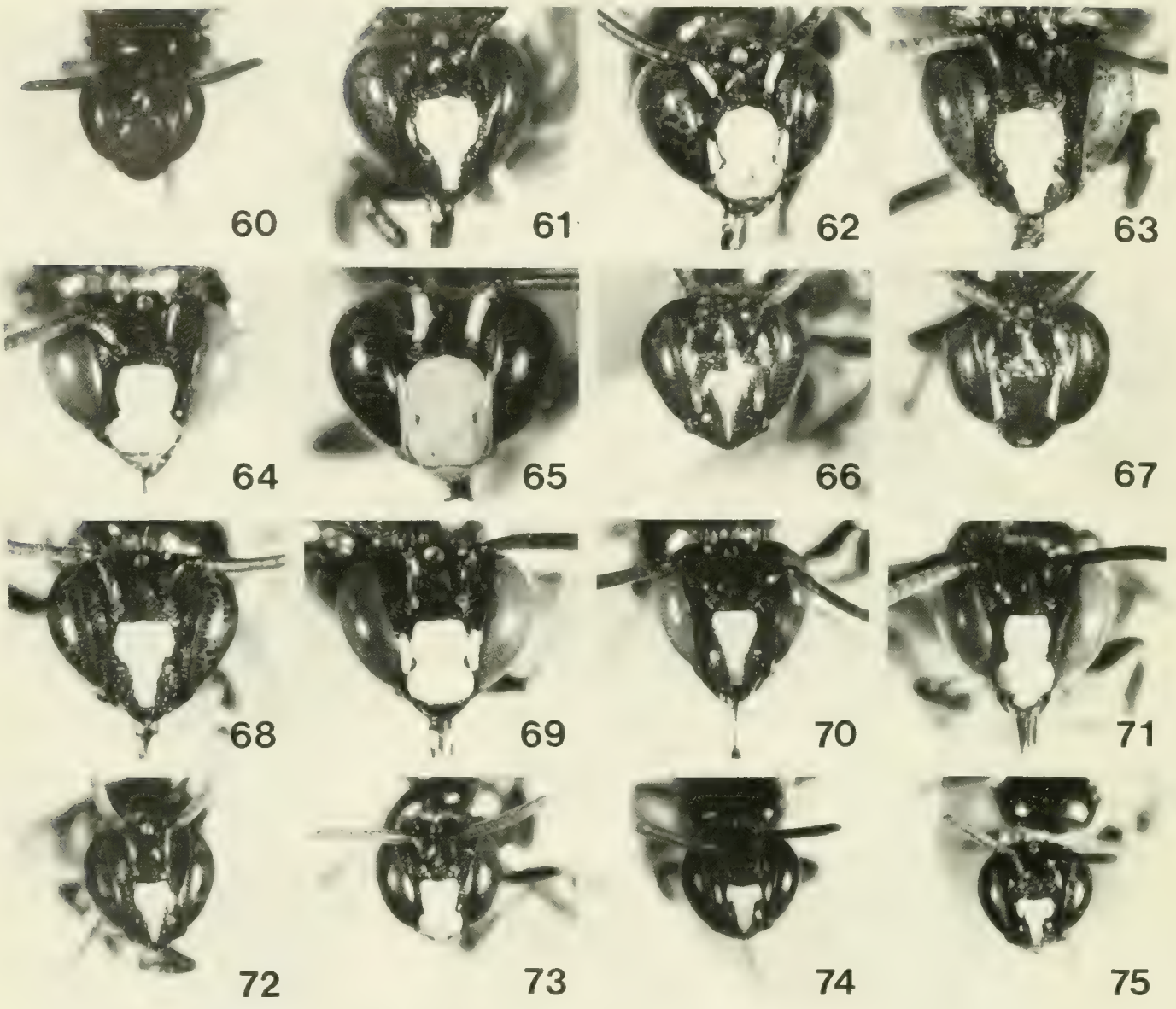
———, ——— and ———. 1992. Laboratory studies on the behavior and colony structure of *Braunsapis hewitti*, a xylocopine bee from Taiwan (Hymenoptera: Anthophoridae). University of Kansas Science Bulletin 54:289-333.

Michener, C. D. 1961. Probable parasitism among Australian bees of the genus *Allodapula* (Hymenoptera, Apoidea, Ceratinini). Annals of the Entomological Society of America 54:532-534.

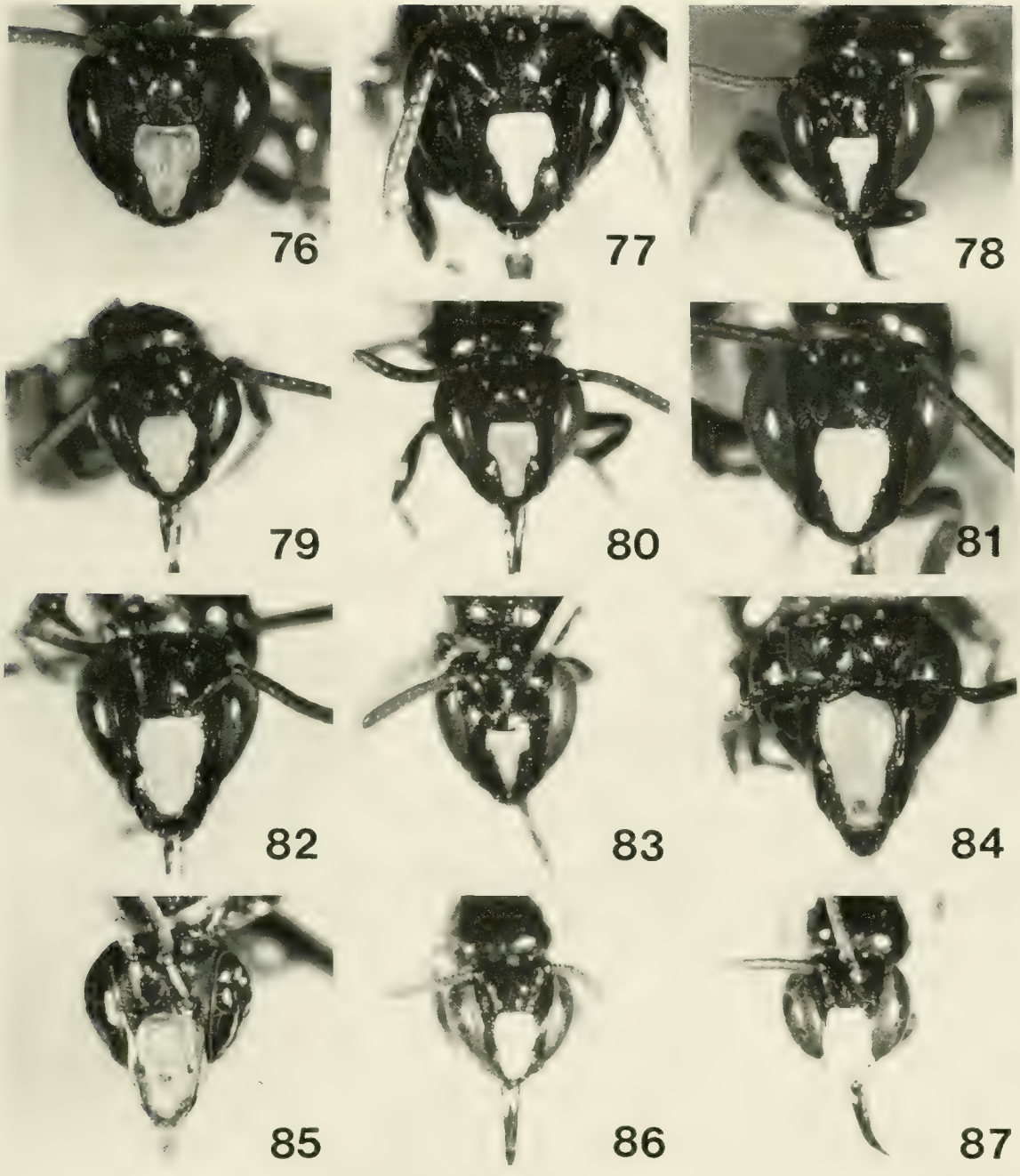
———. 1962. Biological observations on the primitively social bees of the genus "*Allodapula*" in the Australian region (Hymenoptera: Xylocopinae). Insectes Sociaux 9:355-373.
———. 1965. A classification of the bees of the Australian and South Pacific regions. Bulletin of the American Museum of Natural History 130:1-362, pls. 1-15.
———. 1966. Parasitism among Indoaustralian bees of the genus *Allodapula* (Hymenoptera: Ceratinini). Journal of the Kansas Entomological Society 39:705-708.
———. 1968. Biological observations on the primitively social bees (*Allodapula*) from Cameroon. Insectes Sociaux 15:423-434.
———. 1969. African genera of allodapine bees (Hymenoptera: Anthophoridae, Ceratinini). Zoological Journal of the Linnean Society 42:289-293
———. 1970. Social parasites among African allodapine bees (Hymenoptera, Anthophoridae, Ceratinini). Zoological Journal of the Linnean Society (London) 49:199-215.
———. 1971. Biologies of African allodapine bees (Hymenoptera, Xylocopinae). Bulletin of the American Museum of Natural History 145:219-302.
———. 1974. The social behavior of bees. Cambridge: Harvard University Press, xii + 404 pp.
———. 1975. A taxonomic study of African allodapine bees (Hymenoptera, Anthophoridae, Ceratinini). Bulletin of the American Museum of Natural History 155:67-240.
———. 1977. Discordant evolution and classification of allodapine bees. Systematic Zoology 26:32-56.
———. 1990. Caste in Xylocopine bees. pp. 120-144. *In* W. Engels (ed.), Social insects: an evolutionary approach to caste and reproduction. Berlin: Springer Verlag.
——— and I. H. Syed. 1962. Specific characters of the larvae and adults of *Allodapula* in the Australian region (Hymenoptera: Ceratinini). Journal of the Entomological Society of Queensland 1:30-41.
Reyes, S. G. 1991. Revision of the genus *Braunsapis* in the Oriental region (Hymenoptera, Anthophoridae, Allodapini). University of Kansas Science Bulletin 54:179-207.
———. and C. D. Michener. 1990. Observations on a parasitic allodapine bee and its hosts in Java and Malaysia (Hymenoptera, Anthophoridae, Allodapini). Tropical Zoology 3:139-149.
Sakagami, S. F. 1960. Ethological pecularities of the primitive social bees, *Allodape* Lepeltier [sic] and allied genera. Insectes Sociaux 7:231-249.
Smith, F. 1854. Catalogue of hymenopterous insects in the collection of the British Museum. London, 2:199-465, pls. 7-12.
———. 1858. Catalogue of hymenopterous insects collected at Sarawak, Borneo; Mount Ophir, Malacca; and at Singapore, by A.R. Wallace. Journal and Proceedings of the Linnaean Society of London 2:42-130, pls. 1-2.



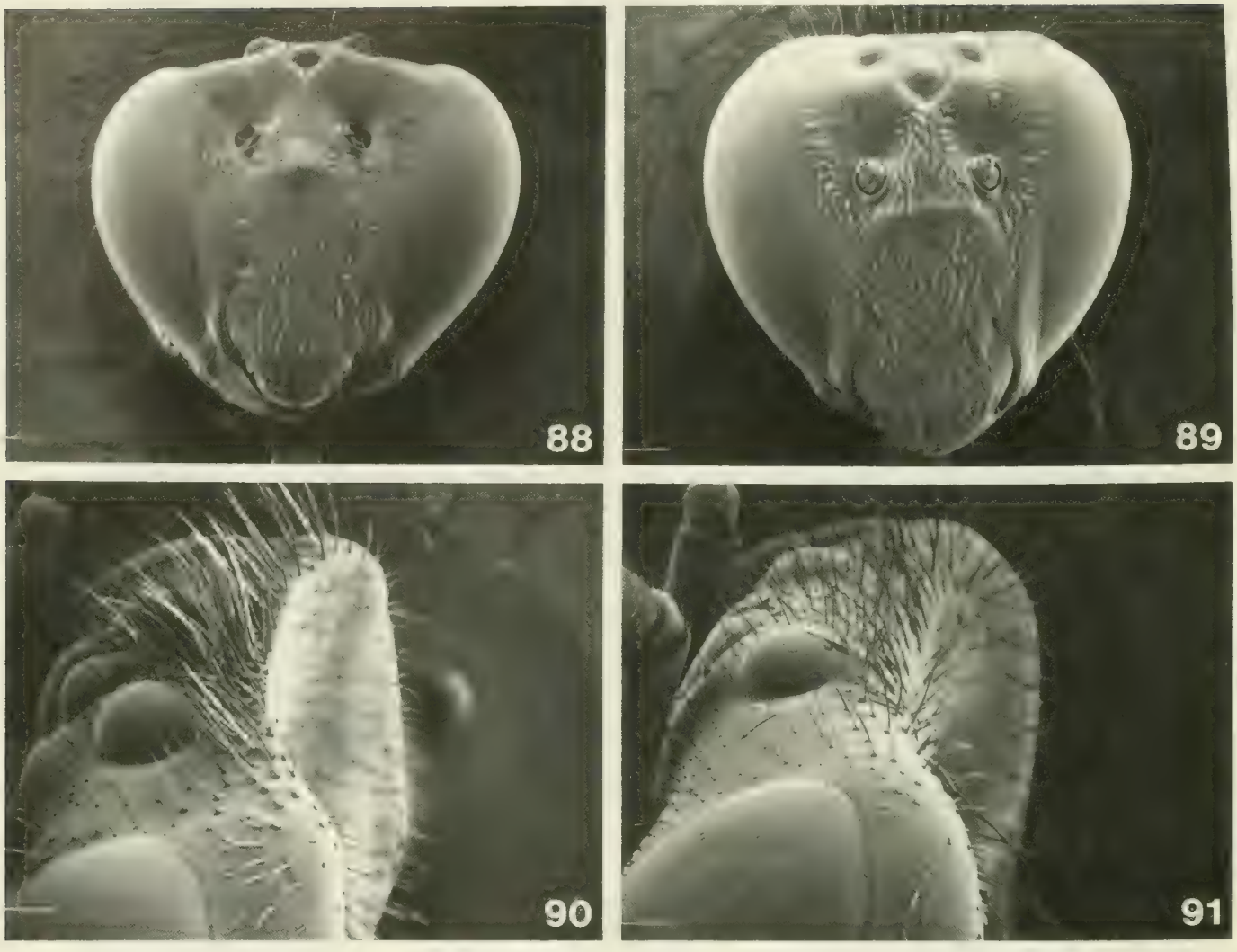
Figs. 48-59. Facial views. **Figs. 48-50.** *B. diminuta*, female from Cooper Creek and males from 12 km NNE of Borroloola and Cooper Creek, Northern Territory, respectively. **Figs. 51-53.** *B. plebeia*, female from Cooktown H'way and males from Thursday Is. (holotype) and Moa Banks Is., 5 km. WSW of St. Pauls, Torres Strait, Queensland, respectively. **Figs. 54-55.** *B. clarissima*, female from Borroloola and male from 14 km. S by E of Mudginbarry HS., Northern Territory. **Fig. 56.** *B. plumosa*, female holotype from 46 km. SSW of Borroloola, Northern Territory. **Figs. 57-58.** *B. diminutoides*, female holotype from Cooper Creek and male paratype from Stuart H'way, Katherine, Northern Territory. **Fig. 59.** *B. anthracina*, female holotype from 6 km. W of Martin's Well, West Kimberly, Western Australia.



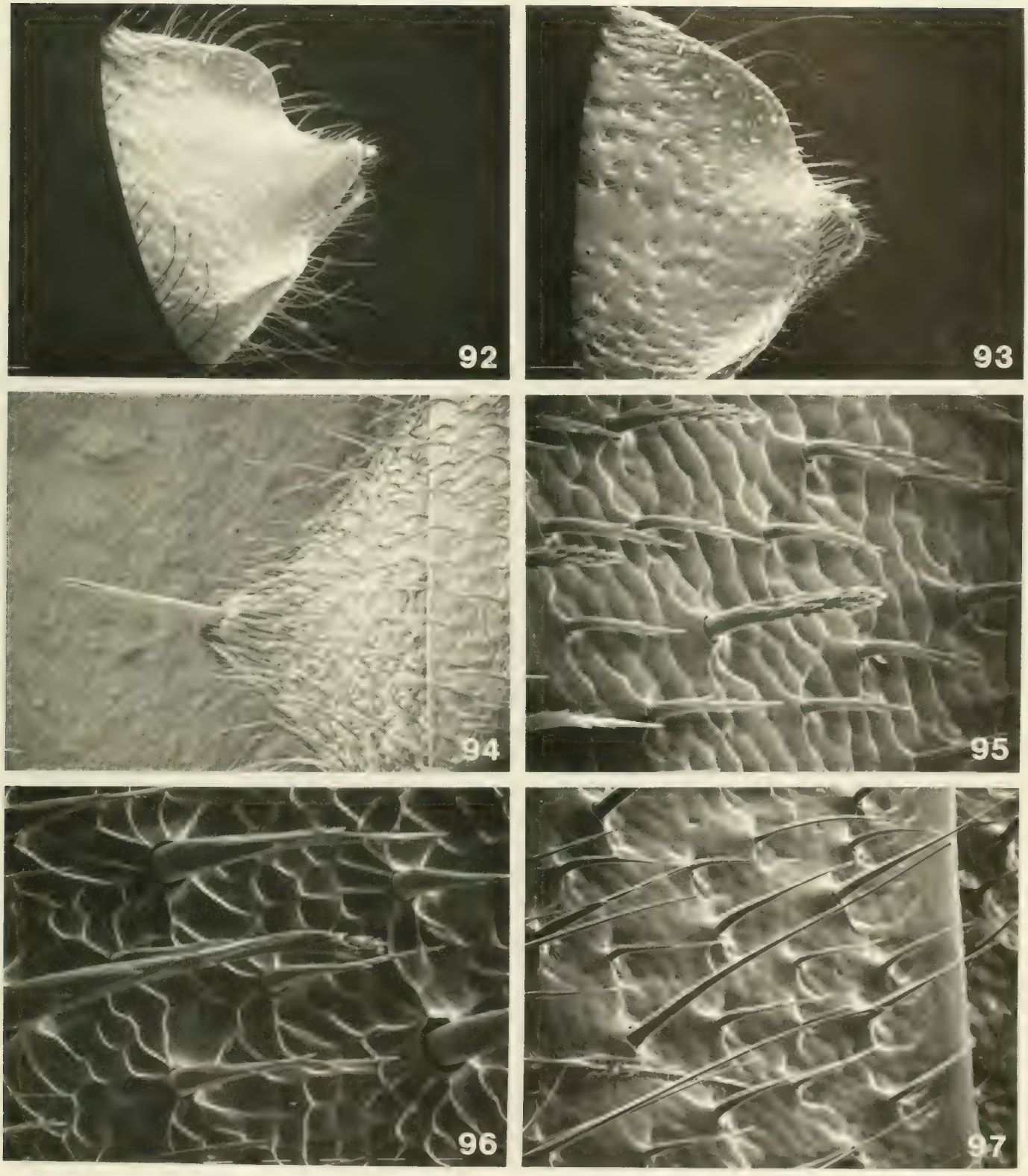
Figs. 60-75. Facial views. **Fig. 60.** *B. anthracina*, male paratype from 6 km. W of Martin's Well, West Kimberly, Western Australia. **Figs. 61-62.** *B. verticalis*, female holotype from Nourlangie Creek, 8 km. N of Mt. Cahill, Western Australia and male paratype from 9 km. N by E of Mudginbarry HS., Northern Territory. **Figs. 63-65.** *B. simillima*, female from Collinsville and males from Bluff Range via Biggenden and Mt. Coot-tha, Queensland, respectively. **Figs. 66-67.** *B. boharti*, female holotype from Tenaru River and male from Honiara, Guadalcanal, Solomon Is. **Figs. 68-69.** *B. protuberans*, female holotype from 2 km E by S of Hidden Valley and male paratype from Bundaberg, Queensland. **Figs. 70-71.** *B. unicolor*, female from 24 km. N by E of Eidsvold and male from Beerburrum, Queensland. **Figs. 72-73.** *B. nitida*, female and male from Black Point, Cobourg Peninsula, Northern Territory. **Figs. 74-75.** *B. biroi*, females from Sattelberg, New Guinea.



Figs. 76-87. Facial views. **Fig. 76.** *B. associata*, female holotype from Mt. Edwards, Queensland. **Fig. 77.** *B. praesumptiosa*, female from Mt. Walsh National Park, Biggenden, Queensland. **Fig. 78.** *B. eximia*, female holotype from Black Point, Cobourg Peninsula, Northern Territory. **Fig. 79.** *B. falcata*, female holotype from Derby, Western Australia. **Fig. 80.** *B. platyura*, female holotype from 8 km. NNW of Taroom, Queensland. **Fig. 81.** *B. hirsuta*, female holotype from Koongarra, 15 km. E of Mt. Cahill, Northern Territory. **Fig. 82.** *B. occidentalis*, female from Cooroboree Rock, Northern Territory. **Fig. 83.** *B. minor*, female holotype from Mackay, Queensland. **Figs. 84-85.** *B. dolichocephala*, female holotype from 56 km. S by E of Alice Springs and male paratype from Arevonga, Northern Territory. **Figs. 86-87.** *B. hyalina*, female holotype and male paratype from 13 km. W of Georgetown, Queensland.



Figs. 88-89. Facial view of female. **Fig. 88.** *B. protuberans.* **Fig. 89.** *B. simillima.* **Figs. 90-91.** Vertex of female. **Fig. 90.** *B. verticalis.* **Fig. 91.** *B. protuberans.*



Figs. 92-94. T6 of female. **Fig. 92.** *B. associata*. **Fig. 93.** *B. praesumptuosa*. **Fig. 94.** *B. diminuta*. **Figs. 95-97.** Hairs on T6. **Fig. 95.** *B. diminuta* (plumose). **Fig. 96.** *B. verticalis* (spiculate). **Fig. 97.** *B. clarissima* (simple).

ANNOUNCEMENT

The *University of Kansas Science Bulletin* (continuation of the *Kansas University Quarterly*) is an outlet for scholarly scientific investigations carried out at the University of Kansas or by University faculty and students. Since its inception, volumes of the *Bulletin* have been variously issued as single bound volumes, as two or three multi-paper parts or as series of individual papers. Issuance is at irregular intervals, with each volume prior to volume 50 approximately 1000 pages in length. Effective with volume 50, page size has been enlarged, reducing the length of each volume to about 750 pages.

The supply of all volumes of the *Kansas University Quarterly* is now exhausted. However, most volumes of the University of Kansas Science Bulletin are still available and are offered, in exchange for similar publications, to learned societies, colleges and universities and other institutions, or may be purchased at $30.00 per volume. Where some of these volumes were issued in parts, individual parts are priced at the rate of 3 cents per page. Current policy, initiated with volume 46, is to issue individual papers as published. Such separata may be purchased individually at the rate of 7 cents per page, with a minimum charge of $1.50 per separate. Subscriptions for forthcoming volumes may be entered at the rate of $30.00 per voluem. All communications regarding exchanges, sales and subscriptions should be addressed to the Exchange Librarian, University of Kansas Libraries, Lawrence, Kansas 66045.

Individual papers for personal use by investigators are available for most recent and many older issues of the Bulletin. Such requests should be directed to the author or to the relevant Museum or Department of the University of Kansas.

The International Standard Serial Number of this publication is US ISSN 0022-8850.

Editor
Charles D. Michener

Editorial Board
Meredith Lane, *Chairman*
James S. Ashe
George W. Byers
Christopher Haufler
Norman A. Slade

THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. 55, Nos. 4 and 5, pp. 123-173 August 30, 1993

NCSU LIBRARY
OCT
HARVARD UNIVERSITY

No. 4. Studies of the Phylogeny and Classification of Long-Tongued Bees (Hymenoptera: Apoidea)

ARTURO ROIG-ALSINA AND CHARLES D. MICHENER

TABLE OF CONTENTS

Abstract 124
Introduction 124
Acknowledgments 125
History of the Classification of Long-Tongued Bees 125
Selection of Taxa 126
Selection of Characters 126
Selection and Coding of Characters of Adults 128
Annotated List of Adult Characters 128
Selection and Coding of Characters of Mature Larvae 138
Annotated List of Larval Characters 140
Phylogenetic Analyses 142
Analysis A, 144; Analysis B, 148; Analysis C, 149; Analysis D, 152; Analysis E, 152; Analysis F-G, 152; Analysis H, 155
Classificatory Results 155
Concluding Remarks 159
Appendix: Number of Tubules in Reproductive Organs 160
Literature Cited 160

No. 5. Phylogenetic Relationships of the Exomalopsini and Ancylini (Hymenoptera: Apidae)

FERNANDO A. SILVEIRA

TABLE OF CONTENTS

Abstract 163
Introduction 163
Acknowledgments 163
Material and Methods 164
Results 165
Exomalopsini, 167; Ancylini, 167; Relationship between Exomalopsini and Ancylini, 168; Relationships among other Apinae, 168
Discussion and Conclusions 169
Literature Cited 172

Studies of the Phylogeny and Classification of Long-Tongued Bees (Hymenoptera: Apoidea)[1]

ARTURO ROIG-ALSINA[2,3] AND CHARLES D. MICHENER[2]

ABSTRACT

Phylogenetic analyses of long-tongued bees were made using up to 82 taxa, 131 adult characters, and 77 larval characters. Only two families of long-tongued bees are recognized, Megachilidae and Apidae. The Pararhophitini and Fideliini form a subfamily, Fideliinae, of Megachilidae. The subfamilies of Apidae recognized are Nomadinae, Xylocopinae, and Apinae. The tribes Isepeolini, Osirini, and Protepeolini are part of the Apinae, not part of the Nomadinae. *Protepeolus* is a junior synonym of *Leiopodus*. The tribes Euglossini, Bombini, Apini, and Meliponini form a distinctive clade arising from within the subfamily Apinae. The Ctenoplectridae is reduced to tribal status within the Apinae. The Exomalopsini of authors is dismembered, forming the tribes Exomalopsini and Tapinotaspini, and the genus *Ancyloscelis* joining the Emphorini as a subtribe. *Eucerinoda* is included in its own subtribe in the Eucerini and the Ancylini are tentatively separate from but close to the Eucerini. New family-group names (tribal and subtribal) proposed are Hexepeolini, Brachynomadini, Tapinotaspini, and Ancyloscelina.

INTRODUCTION

Despite many studies, the classification and phylogeny of bees has never reached a stage at which most authors could agree on one classification and one probable phylogeny. Intuitive processes have led to diverse systems rather than one system. The problem is particularly acute among the long-tongued (hereafter L-T) bees (defined below), the higher taxa of which seem less differentiated than the commonly accepted families (or subfamilies) of short-tongued (S-T) bees. We therefore selected the L-T bees for cladistic study to see if more satisfying results could be obtained.

The L-T bees include the forms often placed in the families Anthophoridae (including Nomadinae and Xylocopinae), Apidae, Fideliidae and the genus *Pararhophites*, and Megachilidae; as discussed below, the family Ctenoplectridae should also be included.

The expressions L-T and S-T are in many ways inappropriate (Michener and Greenberg, 1980; Laroca et al., 1989), for there are L-T bees with short glossae and S-T bees with long glossae. The L-T bees constitute a monophyletic group ordinarily characterized by having the first two segments of the labial palpi elongate and flattened, forming with the galeae a sheath around the long glossa that is involved in the nectar imbibing process. Palpal segments 3 and 4 are small, directed laterally, and not flattened; occasionally they are absent. The monophyly of the L-T bees is further indicated by the other characters on Cladograms 1 and 2 that show L-T bees as the sister group of the Melittidae.

For some time it has been known that among parasitic Allodapini there exist species obviously related to the L-T nonparasitic allodapines but without long flat basal segments of the labial palpi and with the glossa relatively short. This trend reaches its extreme in the South African parasitic genus *Eucondylops* (Michener, 1970). The parasitic allodapines are mostly not known to visit flowers; they must feed in the nests of their host bees, other allodapines. Thus they do not need equipment for extracting nectar from flowers, and appear to have lost it. Likewise, as emphasized by Silveira (in press), the genus *Ancyla*, which visits shallow-flowered Apiaceae (Popov, 1949), has no long flat segments of the labial palpi, and yet it seems to be a close relative of *Tarsalia*, an obvious L-T bee (see Silveira, 1993). Warncke (1979) separated *Ancyla* and *Tarsalia* only subgenerically. Finally, *Ctenoplectra*, often given familial status because of its combination of characteristics of L-T bees with labial palpi of S-T bees (Michener and Greenberg, 1980), clearly is a member of the L-T bee clade (see Results); it probably lost the palpal characteristics of that clade. It follows, then, that our study includes members of the L-T bee clade, whether or not they actually have the long, flattened segments of the labial palpi. Of the three taxa listed above, however, only *Ctenoplectra* was included in the cladistic analysis; the others are too rare to dismember for detailed study and moreover, their relationships to obvious L-T bees are clear (*Eucondylops* to *Allodapula*, *Ancyla* to *Tarsalia*).

In addition to characters of adults, on which earlier classifications have been based, we have considered larval characters; we examine phylogenies based upon adults, upon larvae, and upon the two stages together. In reality, partly

[1] CONTRIBUTION NUMBER 3081 FROM THE DEPARTMENT OF ENTOMOLOGY, UNIVERSITY OF KANSAS, LAWRENCE.
[2] DEPARTMENT OF ENTOMOLOGY AND SNOW ENTOMOLOGICAL MUSEUM, SNOW HALL, UNIVERSITY OF KANSAS, LAWRENCE, KANSAS 66045-2119, USA.
[3] PRESENT ADDRESS: MUSEO ARGENTINO DE CIENCIAS NATURALES "BERNARDINO RIVADAVIA," BUENOS AIRES, ARGENTINA.

because they are still known only from a limited number of taxa, the larvae contributed relatively little to our conclusions.

The following abbreviations are used throughout this work:

L-T	long-tongued
S-T	short-tongued
T1, T2, etc.	first, second, etc. metasomal terga
S1, S2, etc.	first, second, etc. metasomal sterna

In the phylogenetic analyses, L = tree length, T = number of trees, ci = consistency index, and ri = retention index.

ACKNOWLEDGMENTS

Our work was greatly facilitated by National Science Foundation grant BSR 87-16817 (C. D. Michener, principal investigator). Preparation of the cladograms in form for publication was largely by Douglas Yanega. For editorial and bibliographic help, we thank Virginia Ashlock. A. R.-A.'s work in Lawrence was possible thanks to the Organization of American States and the Consejo Nacional de Investigaciones Cientificas y Tecnicas, Republica de Argentina.

We appreciate the opportunity to discuss methodological and other problems with B. Alexander, J. S. Ashe, and S. Reyes of the University of Kansas.

HISTORY OF THE CLASSIFICATION OF LONG-TONGUED BEES

This section is by no means an exhaustive treatment of the history of apoid classification, or classification of L-T bees. We limit ourselves to several classifications to illustrate the diversity of opinions, and to some more recent works that have a direct bearing on our work. We also limit ourselves, in this section, to adult characters since characters of immature stages have not played a major role in bee classification.

In his great work on British bees, Kirby (1802) distinguished L-T from S-T bees, using a generic name for each, *Apis* and *Melitta* respectively. In the same year Latreille (1802) recognized the same two groups as families, the Apiariae and Andrenetae. Subsequent authors such as Smith (1853), Cresson (1887) and Warncke (1977) recognized the same two families, Apidae and Andrenidae.

There were, however, divergent opinions. Lepeletier (1836, 1841) and Schmiedeknecht (1882) classified bees on the basis of habits: solitary, social, and parasitic. There were L-T bees included in each of these three categories. Many subsequent classifications followed this system, placing parasitic bees in separate taxa from the nonparasitic ones. Ashmead (1899) also put all bees that he knew to be parasitic (even *Psithyrus*) in separate families, but these were placed among his families of nonparasitic bees. Tkalců (1972, 1974) revived the idea of separate clades for all parasitic bees (cleptoparasites as well as social parasites like *Psithyrus*), suggesting that they arose from non-pollen-collecting ancestors of the pollen-collecting taxa. This would imply that there were different wasp ancestors for the various major groups of parasitic bees and therefore for groups of other bees as well. To us there is strong evidence for monophyly of all bees (Brothers, 1975), as well as of the L-T bees (Michener and Greenberg, 1980).

Another classification that intermixed L-T and S-T bees was that of Robertson (1904). His was a thoughtful classification, but based almost exclusively on the fauna of a limited region (southern Illinois). It divided bees into two groups of families, those with and those without pygidial plates. Had Robertson studied any of the majority of Colletinae in the world (for example, *Leioproctus*) that have pygidial plates, he would have recognized his error. It is now clear that the plate is an ancestral character that has been lost independently among various lineages of bees as well as wasps, but Robertson's classification was widely accepted for several decades.

We turn now more strictly to the L-T bees. Schenck (1859, 1869) transferred *Ceratina* from the parasitic bees, where it had been placed by Lepeletier (1841), to the Anthophoridae. (He also included the S-T genera *Melitturga* and *Systropha* in the Anthophoridae.) Even Börner (1919) still placed *Ceratina* among the parasitic bees in the Nomadidae. Schenck also separated the parasitic megachilids from the parasitic anthophorids, but did not place either with its nonparasitic relatives. It is relevant to our study that Schenck placed melittids between the S-T families (he called them subfamilies but used the -idae ending) and the L-T families. Thomson (1872) placed most of the parasites in taxa (tribes) with their nonparasitic relatives but associated the melittids (S-T) with *Ceratina* and *Anthophora* in one tribe.

Robertson (1904) was the first to clearly recognize such groups as the Eucerini and Emphorini; he called them families.

Michener (1944) recognized the Lithurginae as quite different from the Megachilinae in spite of similar appearance. He also recognized numerous tribes of Nomadinae, separate from the parasitic Anthophorinae such as the tribe Melectini. He assembled the Melittidae, our principal outgroup for the study of L-T bees, although it had earlier been dispersed in various ways and sometimes associated with rophitine or panurgine genera, and he included *Ctenoplectra* in the Melittidae. He placed the Fideliinae and the Anthophorinae in the Apidae, *Pararhophites* being in the subfamily Anthophorinae. Minor subsequent modifications were summarized by the classification used in Michener (1979). Anthophoridae was unfortunately recognized there as a family separate from Apidae.

Sŭstera (1958) proposed a classification in many ways not too different from those of Michener, but with the Nomadinae divided. The Nomadini, Ammobatini and Pasitini were in the Andrenidae, an S-T family, while the Epeolini, Epeoloidini, and other parasitic anthophorines remained in the Anthophoridae, an L-T family.

Warncke (1977) gave a quite different classification, as noted above, using the two families Apidae and Andrenidae. Like some other authors, he recognized the similarity of Melittidae (an S-T family) to L-T bees, and indeed he placed them (as a subfamily) in the Apidae. *Pararhophites* was in-

cluded in the Melittinae. Other features that seem strange are inclusion of *Exomalopsis* and *Fidelia* in the Ceratininae, and of *Manuelia* and *Xylocopa* with *Ancyla* in one group of Anthophorinae.

Rozen (1977), after studying larvae of Fideliinae, transferred the subfamily to the Megachilidae. McGinley and Rozen (1987) supported the above placement of Fideliinae and Rozen in the same paper placed *Pararhophites* near the Fideliinae in the Megachilidae. These placements are strongly supported by the present study.

Michener and Greenberg (1980) supported the placement of Melittidae as derived from other S-T bees, as indicated by Michener in 1944. They considered Melittidae as the sister group to Ctenoplectridae and the L-T bees together, and separated Ctenoplectridae from the Melittidae as a family of S-T bees with features of L-T bees, and the sister group to the L-T bees. We show that this placement is incorrect in the Phylogenetic Analyses, below.

Sakagami and Michener (1987) proposed the tribe Manueliini in the Xylocopinae, and indicated that the Xylocopinae and the apine clade (meaning Apini, Bombini, Euglossini, and Meliponini) are sister groups. This viewpoint is not supported by the present study.

From this brief and incomplete historical review, the lack of consensus throughout the history of bee classification is clear. Disagreement as to taxonomic rank is of minor importance; recent authors place bees in one, two, or up to eleven families. The interesting disagreements concern inferred phylogenetic relationships, which can be indicated, if desired, within a classification regardless of the taxonomic rank.

SELECTION OF TAXA

The 82 taxa used in our analysis of adults were selected to represent as nearly as possible all subfamilies and tribes of L-T bees and of the outgroup, the Melittidae (Table 1). Where there is considerable diversity within a tribe or subfamily, more than one genus was often selected, particularly if relations within the taxon are poorly understood, as, for example, in the groups that were included in the Exomalopsini (*sensu* Michener and Moure, 1957). Two subgenera of certain genera were included. We believe that the representatives selected provide a good survey of the diversity among L-T bees, although there are only 82 species representing perhaps 10,000 species of L-T bees.

For each genus or subgenus included in the study, a particular species was selected for detailed examination, primarily on the basis of abundance of material. It is characters of such species that are the bases for the phylogenetic discussion and analysis; the species are listed in Table 1. For the sake of brevity we often refer to characters of a genus, tribe, etc., but in reality we mean, of the selected exemplars. Of course we believe that in most cases the characters listed for a species are those of its genus and its tribe, etc., and we have examined the external characters of species other than the exemplars. In some cases we know of interspecific variation in some of the characters used in our study. An alternative approach would have been to analyze generic characters, tribal characters, etc. This would have involved recording characters of many species in order to determine which are the generic characters and would have required exclusion of various characters because most species would not have been available for dismemberment and study of the internal skeletal characters that are involved in our study. Of course if phylogenies were available for each genus, tribe, etc., one would be in a better position to select characters of each for analysis in a broader study. We believe that the use of exemplars is more practical and probably better considering the present state of the study of apoid phylogeny.

When family, subfamily, or tribal names are used, reference is to the taxa as understood in the classification proposed in the section on Classificatory Results.

Unfortunately, because of lack of material for dissection, there remain a few taxa of questionable phylogenetic position that could not be examined in full detail and that are excluded from the analysis. One of these is the genus *Ancyla*. It is perhaps closely related to *Tarsalia* (Silveira, 1993 and in press) and the two were included in the same genus by Warncke (1979). *Ancyla* is interesting principally because of the reduced labial palpi and rather short glossa, as indicated in the Introduction. Another is *Townsendiella;* the Townsendiellini are not represented in our study although the position of this taxon is reasonably well known (see Roig-Alsina, 1991). It would also have been desirable to include *Epeoloides*, presumably a divergent member of the Osirini, sometimes placed in a tribe Epeoloidini. *Dioxys* could well have been included; it is a divergent member of the Anthidiini.

The larval study is largely based on the data recorded by McGinley (1981, Appendix 1). To his table of data we added character states for *Pararhophites* (from McGinley and Rozen, 1987) and *Paratetrapedia* (from Rozen and Michener, 1988), since these are genera of great interest in bee systematics. Fortunately their characters were reported in such a way that the data could easily be extracted and coded to correspond to McGinley's Appendix 1.

The species in the larval study are those listed by McGinley (1981, Table 1), plus *Pararhophites orobinus* (Morawitz) and *Paratetrapedia swainsonae* (Cockerell).

SELECTION OF CHARACTERS

Contrary to the recent practice of one of us (CDM), we use the word *character* for a feature that varies among taxa, and the expression *character state* for the condition of that character in a particular taxon. Thus "head color" is a character, and "head red" indicates a character state. This is contrary to taxonomists' usual usage but is in agreement with both pheneticists' and cladists' usage and has become well established. The resultant double meaning for *character,*

Table 1. List of Taxa Used as Adult Exemplars
Taxa are listed in the same sequence as in the matrix of adult characters (Table 2). The last nine taxa are S-T bees not included in the matrix.

Exemaptis parvula Ogloblin
Teratognatha modesta Ogloblin
Isomalopsis niveata (Friese)
Exomalopsis jenseni Friese
Tapinotaspis (Tapinotaspoides) tucumana (Vachal)
Tapinotaspis (Tapinorhina) caerulea (Friese)
Paratetrapedia (Arhysoceble) melampoda (Moure)
P. (Paratetrapedia) sp. (Chamela, Mex.)
Monoeca lanei (Moure)
Caenonomada brunerii Ashmead
Ancyloscelis apiformis (Fabricius)
Melitoma segmentaria (Fabricius)
Diadasia pereyrae (Holmberg)
Diadasina distincta (Holmberg)
Ptilothrix tricolor (Friese)
Tetrapedia sp. (La Rioja, Arg.)
Coelioxoides waltheriae Ducke
Tarsalia ancyliformis Popov
Eucerinoda gayi (Spinola)
Canephorula apiformis (Friese)
Eucera chrysopyga Pérez
Melissodes agilis Cresson
Svastra obliqua (Say)
Peponapis fervens (Smith)
Anthophora paranensis Holmberg
Habropoda laboriosa (Fabricius); *H. pallida* (Timberlake)
Deltoptila elefas (Friese)
Centris tricolor Friese
Epicharis elegans Smith
Xeromelecta californica (Cresson)
Zacosmia maculata (Cresson)
Thyreus ramosa (Lepeletier)
Ericrocis lata (Cresson)
Mesonychium jenseni (Friese)
Mesoplia rufipes (Perty)
Rhathymus bicolor Lepeletier
Parepeolus aterrimus (Friese)
Ecclitodes stuardi (Ruiz)
Osiris variegatus Smith
Leiopodus lacertinus Smith
Isepeolus vachali Jörgensen
Melectoides triseriatus (Friese)
Neolarra verbesinae (Cockerell)
Caenoprosopis crabronina Holmberg
Oreopasites arizonica Linsley
Triepeolus distinctus (Cresson)
Epeolus compactus Cresson
Rhogepeolus bigibbosus Moure
Holcopasites calliopsidis (Linsley)
Brachynomada sp. (Argentina)
Kelita sp. (Argentina)
Nomada (Pachynomada) utahensis Moalif
N. (Centrias) sp. (Kansas)
Biastes brevicornis (Panzer)
Hexepeolus rhodogyne Linsley and Michener
Manuelia gayi (Spinola)
Xylocopa virginica (Linnaeus)
Ceratina calcarata Robertson; *C. rupestris* Holmberg
Macrogalea candida (Smith)
Braunsapis facialis (Gerstaecker)
Bombus pennsylvanicus (De Geer)
Apis mellifera Linnaeus
Melipona fulva Lepeletier
Partamona cupira (Smith)
Euglossa cordata (Linnaeus)
Eufriesea violacea (Blanchard)
Parathophites orobinus (Morawitz)
Neofidelia profuga Moure and Michener
Parafidelia friesei Brauns
Lithurge apicalis Cresson
Trachusa (Heteranthidium) bequaerti (Schwarz)
Anthidium porterae Cockerell
Hoplitis albifrons (Kirby)
Osmia lignaria Say
Megachile petulans Cresson
Coelioxys octodentata Say
Ctenoplectra fuscipes (Friese)
Macropis steironematis Robertson
Melitta leporina (Panzer)
Dasypoda panzeri Spinola
Hesperapis ilicifoliae (Cockerell); *H. carinata* Stevens
Meganomia gigas Michener

S-T Bees

Andrena erythrogaster Ashmead
Protandrena mexicanorum Cockerell
Lenoproctus delahozi Toro
Colletes inaequalis Say
Caupolicana ruficollis Friese
Dufourea marginata (Cresson)
Nomia triangulifera Vachal
Halictus rubicundus (Christ)
Augochlora pura (Say)

sometimes meaning that which varies and sometimes the condition of a particular taxon, rarely causes confusion, and particularly in the section on classification we regularly refer, for example, to Character 30-1 instead of writing out Character 30, State (1).

Adults of all the included species (Table 1) were not only examined externally, but were treated with 10% KOH (room temperature, for a day or more), dismembered to get appropriate views of interesting structures, and examined and stored in glycerin.

Selection of characters for use in a study such as this is extremely important. We do not know the ideal way of doing so. There is an infinity of characters that might be found and used in a study of a large group such as the L-T bees. We excluded autapomorphies because they do not contribute to knowledge of intertaxon relationships. Characters that seem to be autapomorphic (i.e., are on terminal taxa) on the cladograms also appear somewhere else in the cladogram. We limited ourselves to characters for which a reasonable assumption about polarity could be made. That is, we included no character for which the plesiomorphic state for L-T bees could not be recognized with some degree of confidence by means of outgroup comparisons as described in the next section.

These practices exclude a multitude of characters that might be used in detailed analyses of smaller groups. For example, features of punctation, surface sculpture, facial proportions, distribution and color of pubescence, and details of shape of the hidden sterna and male genitalia might all be polarizable and valuable in a study of a limited taxon, a genus or perhaps a tribe. These characters, however, cannot be polarized for a large taxon like the L-T bees because they vary kaleidoscopically within both the L-T bees and the outgroups. Since it is impossible to pick out a state for such a character that is plesiomorphic relative to the rest of the states, it is not a polarizable character. The problem is identifying similarities that are homologous and determining their points of origin, things that can often be done within a genus or tribe but that become difficult for similar characters in high-ranking taxa.

With the exceptions indicated below, we included all characters that we found for which a strong hypothesis as to the plesiomorphic state could be made. Nearly all of the characters are those of the exoskeleton, but many involve internal ridges and apodemes.

A problem that arises is the possibility of biasing the selection of characters to produce a certain phylogeny or classification. To some degree this may be impossible to avoid

when characters are selected by specialists in the group who have *a priori* ideas about relationships. However, by using all the characters that we found whose polarity could be determined, we hope to have largely avoided this problem. We believe that *a posteriori* searching for characters to produce a desired result is not legitimate. For example, we suspect that the Exomalopsini, which appears as a paraphyletic group in our study, is in reality monophyletic, and as noted in the section on Classificatory Results, some of our characters suggest this, as does a later study by Silveira (1993). We do not believe that it would be legitimate to search for more characters *in order to* establish monophyly of the group; one might thereby fail to find other evidence showing some taxa to have closer relatives in other groups. The proper procedure would be a more detailed study of the Exomalopsini and its relatives, again using *all* characters that can be found that are polarizable within the group of *Exomalopsis* and its relatives.

SELECTION AND CODING OF CHARACTERS OF ADULTS

The principles used in selecting characters are described above. A few characters, however, were omitted even though we know the plesiomorphic states. Among these was number of segments in the maxillary palpi, which is plesiomorphically 6, but is reduced in various taxa to 5, 4, 3, 2, and 1. The reductions are often variable within taxa, even within species, so that coding is difficult; moreover, such reductions can be seen in most higher taxa. For this reason we believed that this character would contribute little to our knowledge of phylogeny of higher taxa. Some characters that we did use in the analysis also proved to be of little value, but we did not have ready knowledge that this would be the case until the study was made.

A character that we omitted from analysis concerns the seriate disannular hairs of the glossa, which we initially coded as follows: (0) Long, divergent. (1) Minute and ordinarily convergent, invaginated inside glossal canal. (2) Absent. There are two rows of seriate hairs; see Michener and Brooks (1984). They are long and divergent in most S-T bees. Because in L-T bees they are often minute, visible only with dissection and a compound microscope, the distinction between States (1) and (2) was not verified for some taxa and the character was therefore excluded from the analyses. For our study the distinction between State (0) and the others would only have added one character to strengthen the differences between S-T bees (including Melittidae) and L-T bees, i.e., it would have added a character to Nodes 3 and 41 of Cladograms 1a, 1b and 2a, 2b. These are already strongly supported nodes. It is in the Nomadinae and similar parasites that the seriate hairs sometimes become especially small, sparse, and even absent.

Another character that was omitted from the analyses was presence or absence of the hind tibial scopa. It is lost in Megachilinae and parasitic bees. We excluded it (and did not reintroduce it) in an early attempt (before the Analyses reported here) to diminish the effect of convergence among parasitic bees.

Polarity was determined by comparison with five genera representing all three subfamilies of Melittidae (Table 1), the principal outgroup. Melittidae was selected as the closest outgroup because it shares a number of characters with L-T bees even though it is an S-T family on the bases of numerous other characters. Its position was well indicated by Michener and Greenberg (1980). Because a melittid character could be a family-level apomorphy, or because of variation among the five melittid taxa, the states of certain characters were also determined for certain species in other S-T families. Taxa of these families used are listed at the end of Table 1. The phylogeny of the S-T families has not been analyzed; we examined members of the Andrenidae, Colletidae and Halictidae relevant to all characters used in our analyses. The Halictidae appears to be derived in many features, and it was therefore principally from examination of Andrenidae and Colletidae that we determined whether polarities based on melittid character states were verified or required modification. When modification seemed appropriate, it is explained in the annotated lists of characters.

The plesiomorphic state was coded (0). For the other states, in characters with two or more other states, no assumption was made as to a phylogenetic sequence of those states; all were run as unordered. There were 37 multistate characters in our analysis of adults and 12 in the analysis of larvae. For individual characters, many of the problems concerning polarity and application of codes are explained in the lists of characters. Some characters relate to structures that are absent in certain taxa. For example, we list characters of the flabellum, a structure that is sometimes absent. In such cases, the character is coded as (?) for taxa lacking the structure. The same code is used if a structure cannot be observed, for example, because of lack of material.

ANNOTATED LIST OF ADULT CHARACTERS

1. Subantennal suture: (0) Directed toward lower margin of antennal socket, sometimes divided (Y-shaped) below socket. (1) Directed toward outer margin of socket. When the suture is Y-shaped, the outer branch is directed toward the outer margin of the socket but the lower, undivided stem is directed toward the lower margin. State (1) is characteristic of Megachilinae.

2. Anterior tentorial pit: (0) High on epistomal suture. (1) At or below middle of lateral part of epistomal suture.

3. Integument of paraocular area: (0) Not differentiated from more median part of frons. (1) Narrow area bordering eye with punctures sparser and smaller than rest of frons, paler in cleared specimens, margins sometimes diffuse. (2) Such an area broad, ovoid, with sharp limits (more distinct in female than in male). Smaller areas, in particular [e.g., State (1)], are not recognizable except in cleared specimens. At least in State (2) there is a layer of possibly glandular tissue underlying the area. Such areas are suggestive of the facial foveae of many colletid and andrenid bees. Our polarization is based on the absence of such areas in Melittidae, but such absence could be a synapomorphy of that family. Their absence also in Megachilidae [although State (1) occurs in Fideliini], Nomadinae and Xylocopinae supports the polarization

indicated above for the L-T bees and especially for the Apidae. State (2) is characteristic of *Exomalopsis*, its allies such as *Eremapis*, and also *Tapinotaspis*.

4. Paraocular carina: (0) Absent. (1) Present.

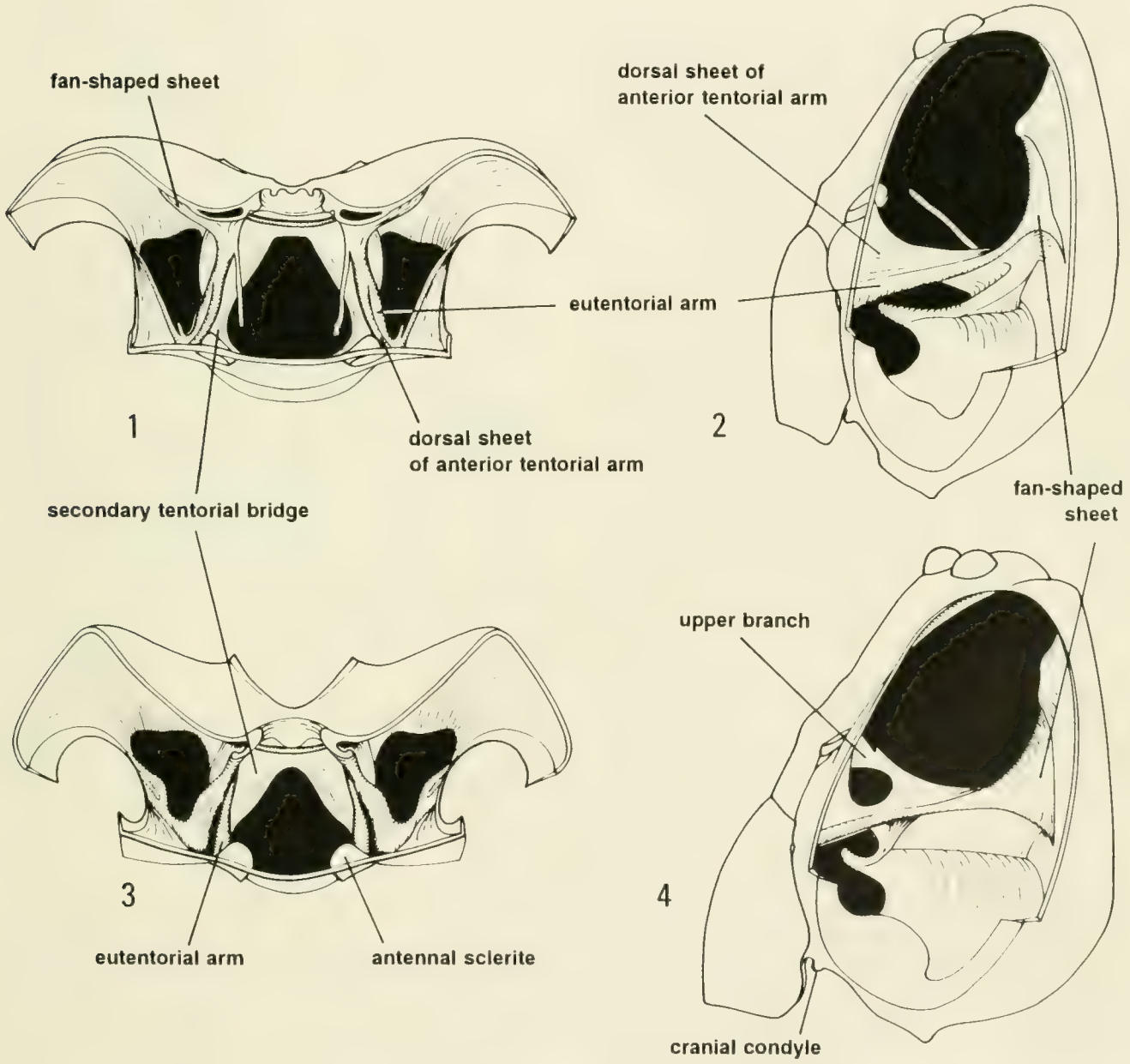
5. Condyle of anterior mandibular articulation (cranial condyle): (0) Contiguous with lateral clypeal margin. (1) Partly covered by lateral clypeal margin, which is usually elevated over condyle (Fig. 4). The melittids (except some *Hesperapis*) exhibit State (1). However, because State (0) characterizes other S-T bees, most melittids appear to be derived in this character.

6. Lateral part of lower portion of clypeus: (0) Not bent backward or only gently curved backward. (1) Strongly and abruptly bent back, so that lateral parts are at angle of 90^0 to 115^0 to median part.

7. Labrum: (0) Broader than long. (1) Longer than broad.

8. Anterior surface of labrum of female: (0) With basal polished area, sometimes elevated, clearly delimited from punctate and hairy disc. (1) Without basal polished area. *Neofidelia* has a short polished area, perhaps equivalent to that described above; it was coded (1), however.

9. Erect labral setae: (0) Not forming a U- or V-shaped row. (1) Coarse setae forming U- or V-shaped row, with midpoint (base of



Figs. 1-4. Head capsule, female; muscles and eyes removed to show tentorial structure. **1.** *Centris tricolor*, transverse section above antennal insertions, view from above. **2.** *Centris tricolor*, head sectioned along paraocular area, lateral view. **3.** *Anthidium porterae*, transverse section above antennal insertions, view from above. **4.** *Melissodes agilis*, head sectioned along paraocular area, lateral view.

U or V) near apex of labrum and lateral arms extending basad near margins of labrum. State (1) occurs in many megachilids.

10. Tuft on apical margin of labrum: (0) Absent. (1) Present. Although present in *Dasypoda*, such a tuft is absent in most S-T bees.

11. Antennal sclerite: (0) Not extending internally beyond antennifer (Figs. 6, 7). (1) Extending internally beyond antennifer (Figs. 9, 10). State (1) is characteristic of Emphorini and *Coelioxoides; Ancyloscelis* is intermediate but was coded (1) like other Emphorini.

12. Dorsal sheet of anterior tentorial arm: (0) Without a branch united with upper wall of antennal socket (Fig. 2). (1) With such a branch (Fig. 4). State (1) is characteristic of Eucerini.

13. Dorsal sheet of anterior tentorial arm: (0) Without spur reaching orbit of eye. (1) With spur reaching laterally to eye margin and indicated externally by transverse line or scar across paraocular area at level of antenna. State (1) is characteristic of Euglossini.

14. Union of anterior tentorial arm to head wall below antennal socket: (0) Reaching lower margin of antennal socket so that no triangular space is enclosed (Fig. 5). (1) Forming triangular space between dorsal sheet of tentorial arm and attachment of thickening of secondary tentorial bridge, but space small and not always recognizable externally by Y-shaped subantennal suture. (2) Space large, forming triangular subantennal area (Fig. 8) recognizable externally between arms of Y-shaped subantennal suture and lower margin of antennal socket. In *Biastes* the dorsal sheet of the anterior tentorial arm ends below the antennal socket, as does the secondary tentorial bridge; it was coded (0). In Euglossini the attachment of the tentorial arm is so modified that it is difficult to code and in *Partamona* the antennae are so close to the epistomal suture that interpretation is difficult. These were coded (?).

15. Thickening of secondary tentorial bridge: (0) Uniting to head wall at or below antennal socket (Fig. 1). (1) Merging with eutentorial arm before reaching head wall (Fig. 3).

16. Lateral expansion of internal thickening above epistomal ridge: (0) At least as wide as half width of socket diameter (Fig. 5). (1) Reduced, less than half width of socket diameter.

17. Clypeus with apical inflection: (0) Present (Figs. 5-10). (1) Reduced to narrow band.

18. Lateral carina of clypeus, along lower part of epistomal suture of male, and associated groove lateral to it: (0) Absent. (1) Present (Ehrenfeld and Rozen, 1977, Fig. 14). State (1) is found only in certain Nomadinae.

19. Epistomal ridge (internal manifestation of epistomal suture): (0) Well developed (Fig. 5). (1) Absent below tentorial pit.

20. Epistomal ridge below tentorial pit: (0) Receiving sheet from eutentorial arm, this sheet margined internally by a thickening (Figs. 6, 7). (1) Receiving such a sheet which is not margined by a thickening. (2) Without a sheet from the eutentorial arm (Figs. 5, 8-10).

21. Postoccipital pouch below foramen magnum: (0) Absent. (1) Shallow. (2) Distinct and deep (Fig. 12). This feature is variable in melittids, but is absent in other S-T bees; (0) is therefore considered plesiomorphic although most melittids were coded (2).

22. Fan-shaped posterior sheets of tentorium, sometimes represented externally by the occipital sulci: (0) Well developed (Figs. 1, 2, 4). (1) Small to absent (Fig. 3).

23. Attachment of secondary tentorial bridge to posterior wall of head (below foramen magnum): (0) Above and separate from hypostoma at upper end of proboscidial fossa, but connected to hypostoma by vertical septum usually manifest externally as vertical black line extending upward from upper end of proboscidial fossa (Fig. 11). (1) As in (0) but vertical line wider, clear, representing thicker septum. (2) Secondary bridge fused directly to hypostoma, thus eliminating vertical black line, fusion evident externally in that lines of attachment of bridge to head wall reach hypostoma at upper end of proboscidial fossa independently and separated by clear zone (Fig. 12). This character is variable in Melittidae but other S-T bees have State (0) except for *Dufourea*, which has State (2).

24. Epistomal suture below anterior tentorial pits: (0) Nearly straight or gently curved or angulate so that sides of clypeus diverge strongly. (1) Extending straight down, then abruptly angulate laterad, so that sides of upper part of clypeus are about parallel.

25. Ventral sclerite of neck: (0) Absent. (1) Present (Roig-Alsina, 1989, Fig. 4). State (1) is found only in Osirini.

26. Articulation of maxillary cardo and stipes: (0) Without small triangular sclerite (Fig. 13). (1) With small (to minute) triangular intercalary sclerite. State (1) is found only in Melittidae but is not found in other bees and appears to be a synapomorphy of that family. It therefore adds nothing to our study.

27. Maxillary stipes with basal process (Winston, 1979, Fig. 2b): (0) Not produced mesally. (1) Produced mesally, elongate. Although State (0) appears in *Apis*, State (1) is in general characteristic of L-T bees and Melittidae (Michener and Greenberg, 1980).

28. Length of stipital comb-bearing concavity: (0) Over one-fourth length of stipes. (1) One-fourth length of stipes or less, deep (Brooks, 1988, Fig. 5). State (1) is found only in Anthophorini.

29. Maxillary stipes with comb in concavity on distal posterior margin: (0) Absent. (1) Present (Fig. 14). When a comb is present it is always in a concavity. Only some Nomadinae have a concavity from which the comb was probably lost.

30. Maxillary stipes with ridge on outer surface: (0) Absent. (1) Present (Fig. 14). There is some variation in this character. For example, in *Melitta, Ctenoplectra,* and *Euglossa,* the ridge is limited to the apical half or third of the stipes. In *Ceratina* the ridge is near the posterior margin of the outer surface instead of near the middle. In *Melipona* there is an angle but no sharp ridge. Although the character is variable in Melittidae, other S-T bees are coded (0), which is therefore considered plesiomorphic.

31. Dististipital process: (0) Absent. (1) Present, curved anteriorly (Fig. 15b; Winston, 1979, Fig. 7b). State (1) is found only in Megachilinae.

32. Maxillary stipes with expansion on distal anterior margin (opposite to comb and concavity): (0) Absent. (1) Present (Fig. 14).

33. Maxillary palpus with brush of hairs on third segment: (0) Absent. (1) Present. State (1) is found only in Emphorini.

34. Maxillary galea with comb on inner surface: (0) Present (Michener, 1981, Figs. 10-13). (1) Absent. This comb is principally a character of S-T bees (including Melittidae) although *Xeromelecta* has a comb. *Deltoptila, Rhathymus,* and *Thyreus* [coded as (1)] have some hairs in this area.

35. Maxillary galea: (0) Without row of bristles. (1) With longitudinal row of bristles on anterior margin of internal surface (Fig. 15b). The row is sometimes limited to the apical third or fourth, as in *Anthophora, Deltoptila, Mesoplia,* and *Zacosmia;* these were all coded as (1).

36. Maxillary galeal blade: (0) Uniformly sclerotized or only narrowly desclerotized near apex. (1) With posterior margin broadly desclerotized almost to base (Fig. 15).

37. Membrane underlying maxillary lacinia: (0) Unsclerotized, not striate. (1) Striate, sometimes weakly sclerotized.

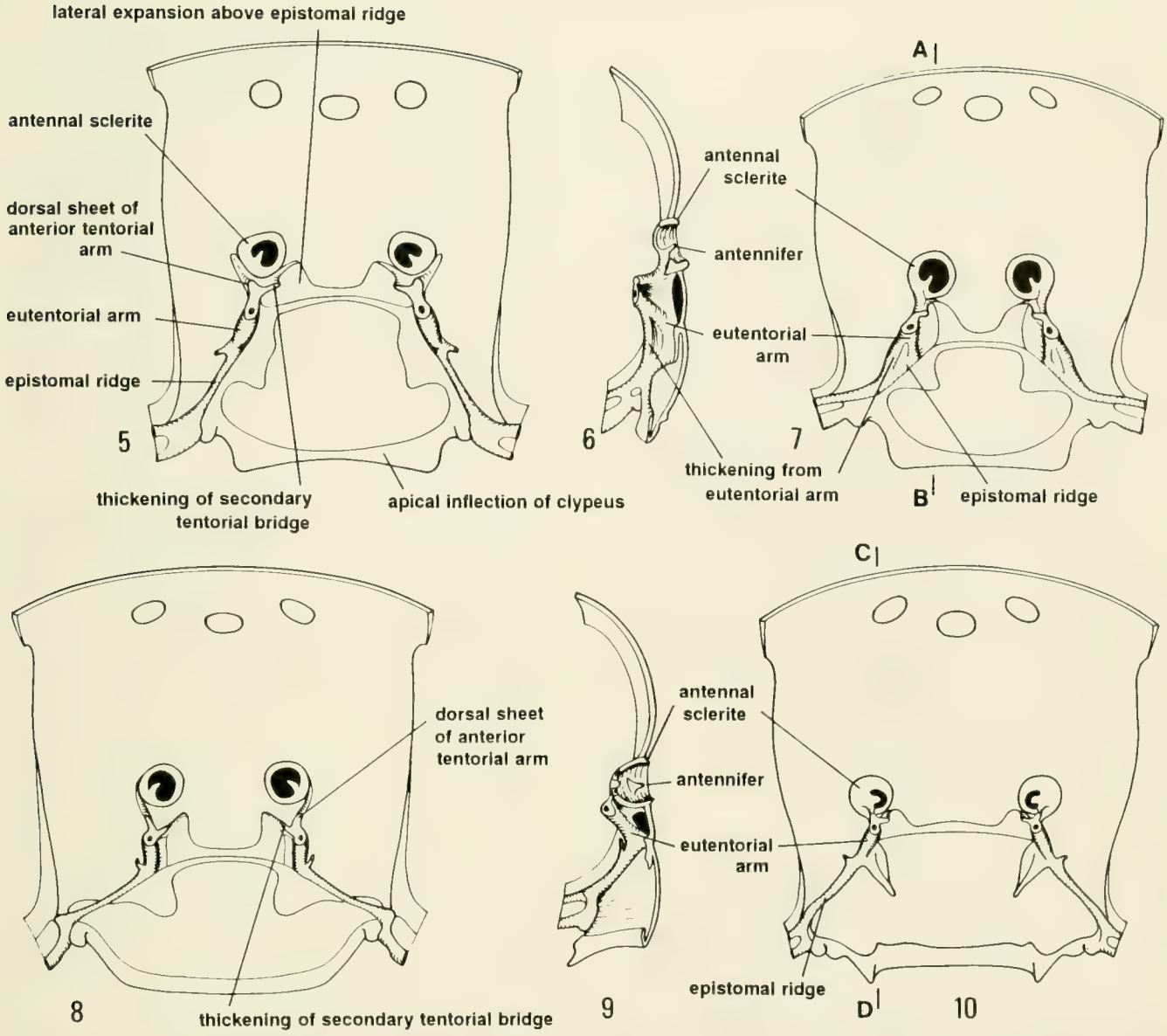
38. Maxillary lacinia: (0) Sclerotized. (1) Membranous.

39. Maxillary lacinia: (0) Rounded. (1) Elongate.

40. Stipital sclerite [terminology of Winston (1979, Fig. 2b)] of maxilla: (0) Distinct. (1) Fused to rest of stipes.

41. Galeal blade (midway between base and apex) with internal sclerotized surface: (0) As wide as external surface. (1) At most two-thirds as wide as external surface (Fig. 15b, c). (2) Three-fourths as wide as external surface or more but narrower than external surface. When the internal surface is narrower than the outer, the anterior edge of the former often appears as a dark line which is the midrib of the galea of Winston (1979).

42. Lorum: (0) Platelike, flat or bent around base of mentum (Michener, 1985, Fig. 31). (1) V-shaped with slender arms (Michener, 1985, Fig. 45). State (1) is characteristic of Melittidae and L-T bees, i.e., of all taxa in our analysis [see Michener and Greenberg (1980)]. This character therefore does not contribute to our analysis.



Figs. 5-10. Anterior wall of the head, female; heads sectioned at level of anterior mandibular articulations. 5, 7, 8, 10, posterior (internal) views; 6, 9, longitudinal sections of 7 and 10 on planes AB and CD, respectively. **5.** *Centris tricolor.* **6, 7.** *Macropis steironematis.* **8.** *Tapinotaspis tucumana.* **9, 10.** *Diadasia pereyrae.*

43. Lorum and mentum: (0) United. (1) Separated from one another.

44. Base of lorum: (0) Simple. (1) With a longitudinal fissure on each side (Plant and Paulus, 1987, Fig. 12).

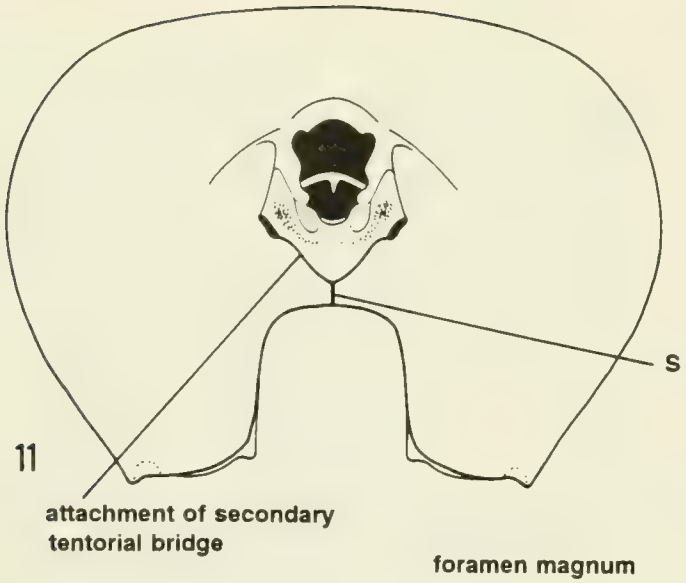
45. Base of prementum: (0) With a fragmentum isolated or partly isolated from rest of prementum (Michener, 1985, Fig. 43). (1) Without such a fragmentum. In *Bombus, Centris, Diadasina, Epicharis,* and *Ptilothrix* there is a projection from the base of the prementum; they were coded (1). For bees as a whole, lack of a fragmentum must be plesiomorphic since there is no fragmentum in most S-T bees. However, it is present in Melittidae and Andrenidae. We therefore consider presence of a fragmentum as plesiomorphic for L-T bees.

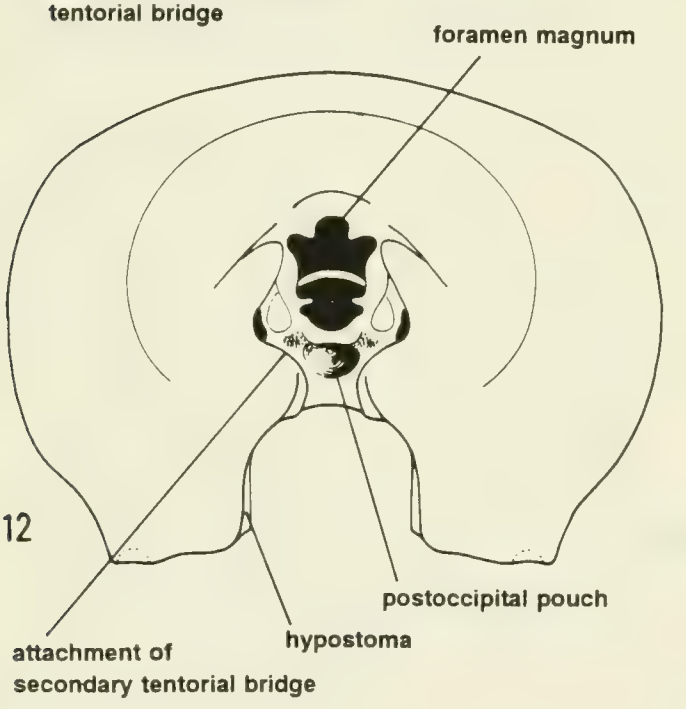
46. Subligular process of prementum (Winston, 1979, Fig. 2c): (0) Fully sclerotized and united to rest of prementum (Fig. 16). (1) Separated from rest of prementum by weak line. (2) Weakly sclerotized.

47. Small sclerite lateral to subligular process of prementum: (0) Absent. (1) Present (Fig. 16). These sclerites are quite distinct in *Leiopodus* and *Ancyloscelis* but are weakly sclerotized and difficult to see in other genera coded (1).

48. Labial palpus segments 1 and 2: (0) Not particularly flattened, similar in form and length to segments 3 and 4. (1) Greatly elongated compared to segments 3 and 4, usually flattened. State (1) is characteristic of L-T bees in general. The first palpal segment in *Lithurge* is short, similar to that of a melittid, although the second segment is long and flat. *Lithurge* was coded (0).

49. Labial palpus, base of segment 1: (0) Parallel sided. (1) Inner margin incised so that base is strongly narrowed (Fig. 16; Winston, 1979, Fig. 35).





Figs. 11, 12. Head capsule, female, posterior view. **11.** *Macropis steironematis;* S, line corresponding to internal vertical septum. **12.** *Melitoma segmentaria.*

50. First segment of labial palpus: (0) Without membranous margin (Figs. 16, 17a, b). (1) With membranous inner margin (Fig. 17c, d).

51. Disannulate surface of glossa: (0) Exposed, nearly as large as annulate surface (Michener and Brooks, 1984, Fig. 5). (1) Invaginated, annulate surface surrounding almost whole glossa (Michener and Brooks, 1984, Fig. 8). In various parasitic taxa (e.g., *Isepeolus, Leiopodus, Nomada, Triepeolus,* and *Xeromelecta*) the disannular surface is considerably exposed. It is nonetheless much smaller than the annular surface and the degree of exposure is difficult to assess. Such forms were coded as (1).

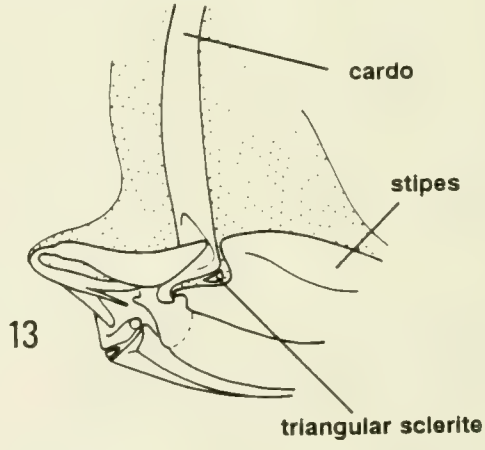
52. Glossal rod (Michener and Brooks, 1984, Fig. 9): (0) Absent. (1) Present but not enclosing bacular canal. (2) Present and partly surrounding the bacular canal (Michener and Brooks, 1984, Fig. 89). For terminology, see Michener and Brooks (1984). State (1) is found in sphecids and most S-T bees including melittids. In most Melectini and Nomadinae the rod is weakly sclerotized and thin (i.e., flat). Such forms are coded as (1), even though the rod seems to be reduced. Michener and Brooks (1984) considered the rod absent in some Nomadinae, but we found at least a stiffer strip in all whose glossae we dissected. There are all degrees of reduction, and the rod is well developed in *Caenoprosopis, Thalestria* and *Triepeolus* in the Nomadinae, as well as in other parasitic forms such as *Leiopodus* and *Isepeolus*. State (2) is rare outside the apine clade; it is not associated with heavy pigmentation in spite of the large size of the rod (see Michener and Brooks, 1984).

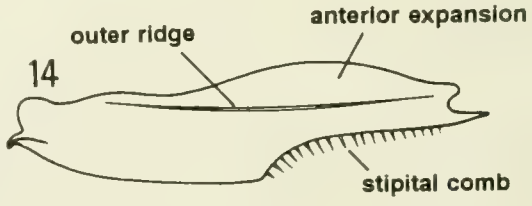
53. Flabellum (Michener and Brooks, 1984, Fig. 8): (0) Absent. (1) A flabellum-like structure present but not constricted at its base. (2) Present, constricted at its base. A flabellum is absent in most S-T bees including most melittids. There are all degrees of flabellar development, of which we recognize two levels, (1) and (2). Presence of a well-developed flabellum in some panurgine Andrenidae presumably shows that it can arise independently. It can also be lost, as in *Habropoda,* where its absence is an autapomorphy rather than a plesiomorphy.

54. Posterior surface of flabellum: (0) Smooth or nearly so. (1) With a cobblestone pattern (Michener and Brooks, 1984, Fig. 94F). Except on the flabellum-like structure of *Dasyposa* (Melittidae), there is nothing among S-T bees to suggest a cobblestone pattern.

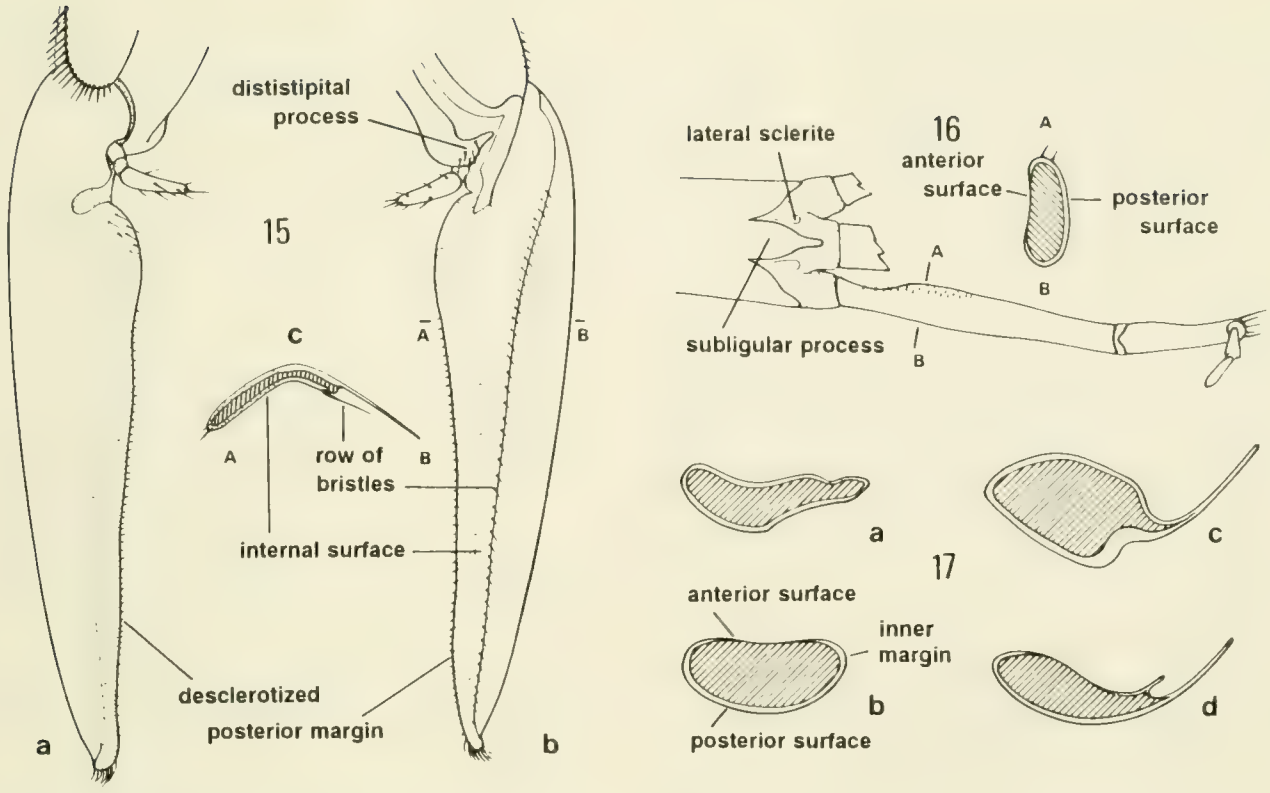
55. Annular hairs of glossa: (0) Extending to base of flabellum. (1) Separated from flabellum by a non-annulate shank (Michener and Brooks, 1984, Fig. 99B). Incompletely developed flabella are always set among the distal annular hairs, as are many fully developed flabella with basal constrictions. In a few taxa the fully developed flabellum is at the end of a largely bare shank.

56. Basiglossal sclerite (Michener and Brooks, 1984, Fig. 7): (0)





Figs. 13, 14: 13. *Macropis steironematis,* posterolateral view of portion of proboscis showing articulation of cardo, stipes and lorum. **14.** *Melitoma segmentaria,* stipes, external view.



Figs. 15-17: 15. *Anthidium porterae*, female. Maxillary galea: a, external view; b, internal view; c, cross section near basal third, at plane AB. **16.** *Tapinotaspis caerulea*, labial palpus and apex of prementum, posterior view and cross section of labial palpus near base. **17.** Cross sections of first segment of labial palpus near basal fourth: a, *Anthidium porterae*; b, *Melitoma segmentaria*; c, *Bombus pennsylvanicus*; d, *Habropoda laboriosa*.

A transverse band across base of glossa. (1) More elongate, often longer than broad (sometimes medially cleft), laterally with posterior basal process extending around side of base of glossa. S-T bees have State (0).

57. Flabellum: (0) Not divided. (1) Divided into preflabellum and postflabellum arising from preapical anterior surface of preflabellum (Michener and Brooks, 1984, Fig. 96F). State (1) is characteristic of Ericrocidini.

58. Paraglossa beyond apex of suspensorium: (0) Shorter than to 1.3 times length of suspensorium. (1) 1.5 to 2.5 times length of suspensorium. (2) Over 3 times length of suspensorium. In melittids the range is up to 1.2. State (2) is characteristic of the Eucerini.

59. Mandibular apex of female: (0) Simple or with lower tooth longer than others. (1) With lower tooth, formed from end of adductor ridge, shorter than next tooth, the mandible being tridentate with middle tooth longest (Michener and Fraser, 1978, Figs. 22, 29). State (1) is found in *Lithurge* and some Xylocopinae.

60. Mandible of female: (0) Slender, region of pollex not expanded distally (Michener and Fraser, 1978, Fig. 12). (1) With region of pollex expanded to form two to several teeth or an edentate margin above rutellum (Michener and Fraser, 1978, Figs. 34, 41). State (1) is characteristic of Megachilidae and at least some members of the apine clade.

61. Mandibular grooves and ridges on outer surface: (0) Distinct. (1) Largely absent. State (1) is found only in the Meliponini and Apini.

62. Pronotum with ventrolateral extensions: (0) Fused midventrally, usually on internal surfaces of extensions. (1) Separated midventrally (Fig. 18). This character is variable in Melittidae but colletids, andrenids, and *Dufourea* in the Halictidae show State (0).

63. Lateral carina separating exposed part of propleuron from part hidden by pronotum: (0) Present (Fig. 19). (1) Absent.

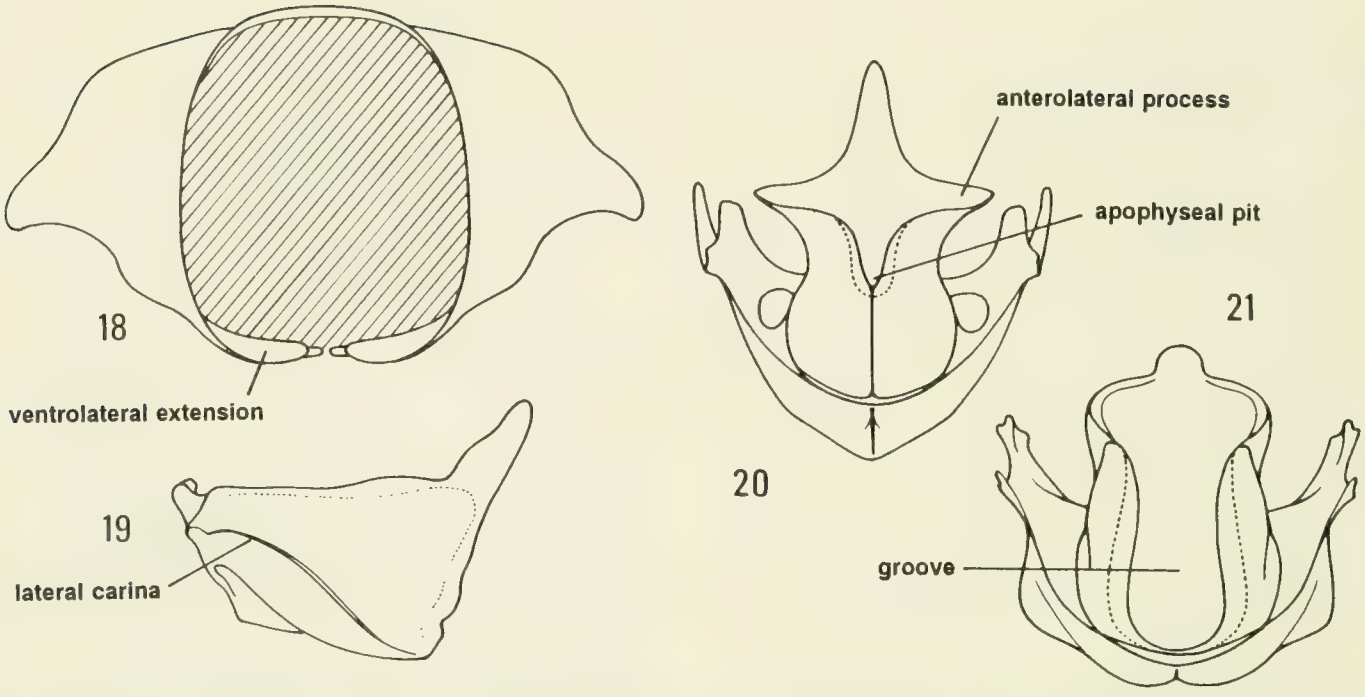
64. Apophyseal arms of prosternum: (0) Fused along median crest. (1) Separate from one another (Michener, 1944, Fig. 26). Although melittids were all coded (1), all other S-T bees show State (0). Presumably State (1) is an apomorphy for melittids and for some L-T bees.

65. Apophyseal pit of prosternum: (0) Present, near middle of prosternum (Fig. 20). (1) Expanded to posterior extremity of prosternum as broad groove (Fig. 21). (2) Absent.

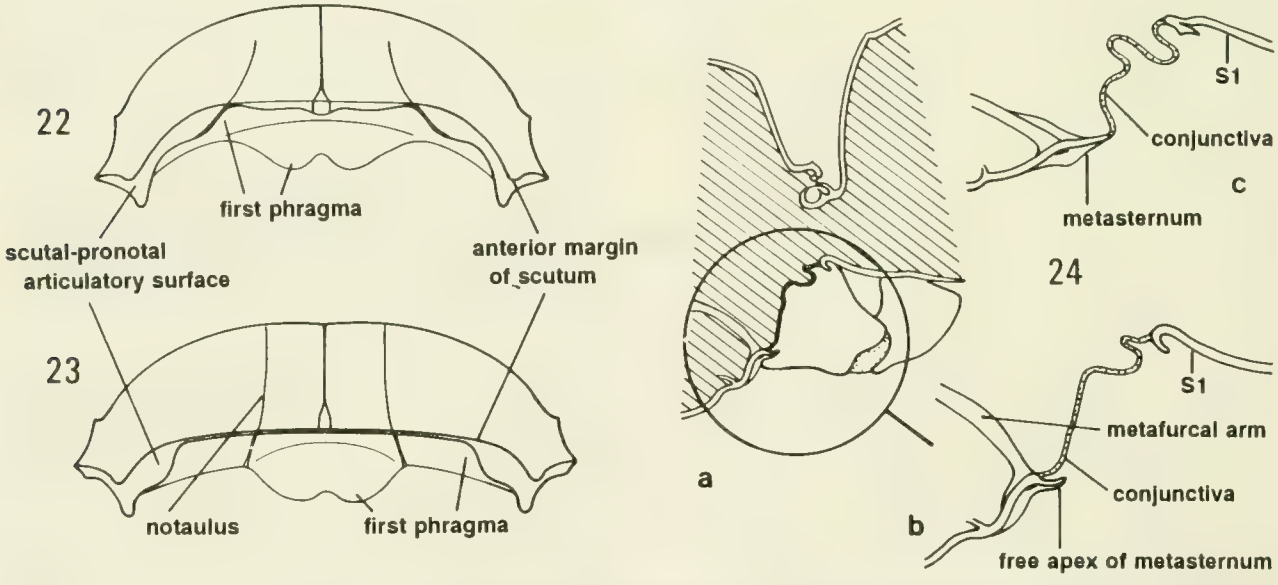
66. Prosternal shape: (0) Not or moderately constricted medially, anterolateral processes shorter and less attenuate (Fig. 20). (1) Strongly and acutely constricted in front of middle, anterolateral processes large and attenuate laterally (Prentice, 1991, Fig. 3.3). State (1) is found only in Apini and Meliponini.

67. First phragma: (0) Not bearing anterior end of internal ridge representing notaulus (Fig. 22). (1) Bearing on posterior surface anterior end of notaular ridge (Fig. 23).

68. Pre-episternal internal ridge (corresponding at least in part to external pre-episternal groove): (0) Directed anteroventrally, more or less straight, reaching down to or surpassing level of pleural scrobe. (1) Curved posteriorly toward scrobe; in this case the corresponding external groove demarks the anterior and lower margins of the swollen hypoepimeral area. (2) Short, not reaching level of scrobe, so that one cannot tell whether it is straight (0) or curved (1). (3) Absent. A long, straight ridge is present in most S-T bees, even though Melittidae exhibit State (3), presumably as a synapomorphy for the family. Presence of such a ridge is therefore considered plesiomorphic. In L-T bees, however, such a ridge is long only in *Caenoprosopis*, *Neofidelia* and *Oreopasites*,



Figs. 18-21: 18. *Melissodes agilis*, female; pronotum, anterior view. **19.** *Melitoma segmentaria*, female; propleuron, lateral view. **20.** Prosternum, female, ventral view, *Melissodes agilis*. **21.** Same, *Mesonychium jenseni*.



Figs. 22-24: 22. Scutum, female, anterior view, *Canephorula apiformis*. **23.** Same, *Melitoma segmentaria*. **24.** Articulation between mesosoma and metasoma, sagittal section; a, b, *Melissodes agilis;* c, *Paratetrapedia* sp.

and is present but only slightly surpasses the level of the scrobe in *Leiopodus* and *Isepeolus*. These taxa are so diverse that one wonders if the ridge may have arisen independently in certain cases. If so, our polarization, while correct for bees as a whole, is wrong for L-T bees. In this case, State (3), as in Melittidae, should be considered plesiomorphic.

69. Internal scrobal ridge from mesepisternal scrobe posteriorly to intersegmental suture: (0) Absent. (1) Present. Although melittids are variable in this character, other S-T bees have State (0).

70. Breadth of metapleuron at level of upper metapleural pit divided by height of metapleuron measured from lower end to apex of wing process: (0) 0.20 or more. (1) 0.19 or less. In Melittidae and other S-T bees the ratio is 0.21 to 0.30.

71. Distance between metapleural pits divided by height of metapleuron (measured as for Character 70): (0) Over 0.20. (1)

0.10 to 0.19. (2) 0.09 or less. The pits are far apart in Melittidae (0.20 to 0.35) and other S-T bees.

72. Membrane closing space behind metasternum and hind coxae and extending to base of S1: (0) Arising above free apex of metasternum on ridge between the hind coxal condyles (Fig. 24a, b). (1) Arising from apical margin of metasternum, which therefore is not free (Fig. 24c). In *Apis, Braunsapis, Ceratina,* Euglossini, and *Parafidelia* the free part of the metasternum is very short, but they are coded as (0).

73. Propodeal profile: (0) With a nearly horizontal basal zone, behind which it rather abruptly turns downward to form the declivous posterior surface. (1) With a steeply slanting or sometimes convex basal zone or entirely declivous. This character is variable in Melittidae as in some other major bee taxa, but State (0) is so prevalent among S-T bees as well as sphecoid wasps that it must be plesiomorphic.

74. Profile of metanotum (and scutellum): (0) Subhorizontal or slanting, scutellum frequently convex but also basically subhorizontal or slanting. (1) Vertical, not overhung by convex scutellum whose posterior margin is more or less vertical. (2) Vertical, strongly overhung by scutellum whose posterior margin faces more or less downward.

75. Lower extremity of metapostnotum (propodeal triangle) internally: (0) With vertical longitudinal ridge (third phragma) whose lower end is above marginal area of propodeum (Fig. 25). (1) With longitudinal ridge extending downward to marginal area of propodeum. (2) With ridge extending beyond marginal area of propodeum as acute point visible through propodeal articulating orifice when the metasoma is removed (Fig. 26), the ridge sometimes largely absent but point clearly visible. (3) Absent.

76. Hind coxal articulation: (0) Clearly above submarginal groove of propodeum-metapleuron (Fig. 25). (1) At or below level of submarginal groove (Fig. 26).

77. Articulation of propodeum with T1: (0) Forming a simple tooth at each side of articulating orifice (Figs. 25, 26). (1) Forming two teeth at each side of articulating orifice (Fig. 27). State (1) is found only in Anthophorini.

78. Conjunctiva between metasternum, hind coxae, and S1: (0) Entirely membranous. (1) With sclerotized bars near coxal margins, meeting one another or fused near posterior point of metasternum (Snodgrass, 1956, Fig. 33C). The sclerotized bars suggest a remnant of the propodeal sternum, present in many wasps, apparently lost in bees. State (1) is found only in certain members of the apine clade.

79. Metapostnotum (propodeal triangle) with hairs: (0) Absent. (1) Present and widespread. State (0) is found in most S-T bees including the Melittidae.

80. Hind trochanter with inner basal surface: (0) Angulate (Fig. 29). (1) Rounded (Fig. 28). State (0) is frequent in S-T bees.

81. Degree of isolation of bases of hind tibial spurs by sclerotized bridges around articulations of spurs: (0) None to partial (Cane's [1979] codes 0 to 2). (1) Almost complete (Cane's code 2+ for both spurs). (2) Complete, with sclerotic bridge between spur bases (Cane's code 3 for both spurs). Like melittids, other S-T bees exhibit State (0).

82. Inner margin of inner hind tibial spur of female: (0) Finely serrate to ciliate (coarsely serrate in Fideliinae). (1) Pectinate, with long, strong teeth. Many S-T bees, including melittids, exhibit State (0).

83. Outer hind tibial spur (usually inner also) of female: (0) Finely serrate or ciliate. (1) Coarsely serrate. (2) Absent.

84. Basitibial plate: (0) Present at least in female. (1) Absent.

85. Hind tibial scopa (female): (0) Absent or consisting of uniformly dispersed hairs on outer side of tibia, i.e., corbicula absent. (1) Surrounding large polished space on outer side of tibia, i.e., corbicula. State (1) is found in the apine clade and in *Canephorula* in the Eucerini.

86. Apex of inner surface of hind tibia (female): (0) Without comb of bristles. (1) With comb of bristles, i.e., the rastellum. State (1) is found in the apine clade.

87. Apex of hind tibia (female): (0) Not expanded dorsally, so that basitarsus is articulated near dorsal margin and appears to arise near middle of apex of tibia. (1) Expanded dorsally, so that basitarsus is articulated away from dorsal margin. The expansion [found only in the apine clade, except slightly present in *Ctenoplectra,* coded (1)] is perhaps an aspect of broadening the tibia for a corbicula, but does not occur in *Canephorula.*

88. Base of hind basitarsus (female): (0) Not broadened. (1) Widened to form the auricle which pushes pollen up into corbicula. State (1) occurs only in the Apini, Bombini and Euglossini. In Euglossini the structure is quite different and it may not be homologous to the auricle of Apini and Bombini.

89. Hind basitarsus (female): (0) Giving rise to second tarsomere at apex. (1) Projecting distad above articulation of second tarsomere as process without an apical brush. (2) Projecting distad as in (1) but ending in a small dense brush (penicillus). The polarity indicated above is based on State (0) in our outgroup, the Melittidae. However, many S-T bees have a penicillus. If the loss of the penicillus and process is a melittid apomorphy, then State (2) or possibly (1) would be the proper plesiomorphic condition for L-T bees.

90. Shape of hind basitarsus (female): (0) Over 3.0 times as long as wide. (1) 1.5 times as long as wide or less. (2) 1.6 to 2.9 times as long as wide, i.e., intermediate. This character is variable in Melittidae but the other S-T bees studied, except *Caupolicana,* have State (0).

91. Under surface of middle tibia of female: (0) With oblique longitudinal ridge bearing a longitudinal brush (mid tibial comb of Jander, 1976) of hairs (Fig. 30). (1) Flat, with more scattered hairs (Fig. 31). This character is variable in melittids; polarization is based on the prevalence of State (0) in other S-T bees.

92. Middle tibial spur: (0) Finely serrate or ciliate, with apex simple. (1) Coarsely serrate, with apex simple. (2) Serrate but ending in two to several large teeth or spines. State (2) is characteristic of Ericrocidini.

93. Row of stout setae on middle basitarsus (female): (0) Absent. (1) Present (Neff and Simpson, 1981, Fig. 5). State (1) is a feature of some oil-collecting bees.

94. Front basitarsal comb of female, a row of strong setae extending from apex of strigilar concavity nearly to apex of tarsomere, distal part of comb curved: (0) Absent. (1) Present (Neff and Simpson, 1981, Fig. 13). This is a feature of some oil-collecting bees. Similar combs in different positions on the basitarsus are present in *Tetrapedia* and *Paratetrapedia.* They are autapomorphies and therefore not included in the analysis.

95. Trunk of anterior tibial spur: (0) Simple. (1) With low expansion at right angles to velum, curving apically into spine of malus. (2) With strong expansion at right angles to velum, ending in strong angle or prong (Schönitzer and Renner, 1980, Fig. 19). The expansion described for State (2) is the anterior velum of Schönitzer (1986).

96. Velum of anterior tibial spur: (0) Narrow, 1.5 or more times longer than wide, usually lenticular, thus widest near middle. (1) Broad, 1.10 to 1.45 times as long as broad, quadrate. (2) About as long as broad (0.95-1.05). Although this character varies in Melittidae, the frequency of State (0) in other S-T bees justifies our polarization (see Schönitzer, 1986).

97. Anterior coxa with carina along inner margin, frequently bending laterad at base and extending partway across base of coxa: (0) Absent. (1) Present (Roig-Alsina, 1989, Fig. 4). State (1) is characteristic of Osirini.

98. Arolia: (0) Present. (1) Absent.

99. Claws of female: (0) Cleft, inner ramus sometimes a tooth. (1) Simple. Forms with the lower ramus broad, flattened, and blunt are nonetheless coded (0).

100. Number of submarginal cells in forewing: (0) Three. (1) Two. (2) None clearly defined, although faint veins often present. State (2) is characteristic of Meliponini. Although variable in Melittidae, State (0) is so common in S-T bees and in wasps that it is clearly plesiomorphic. Reduction to two cells has occurred inde-

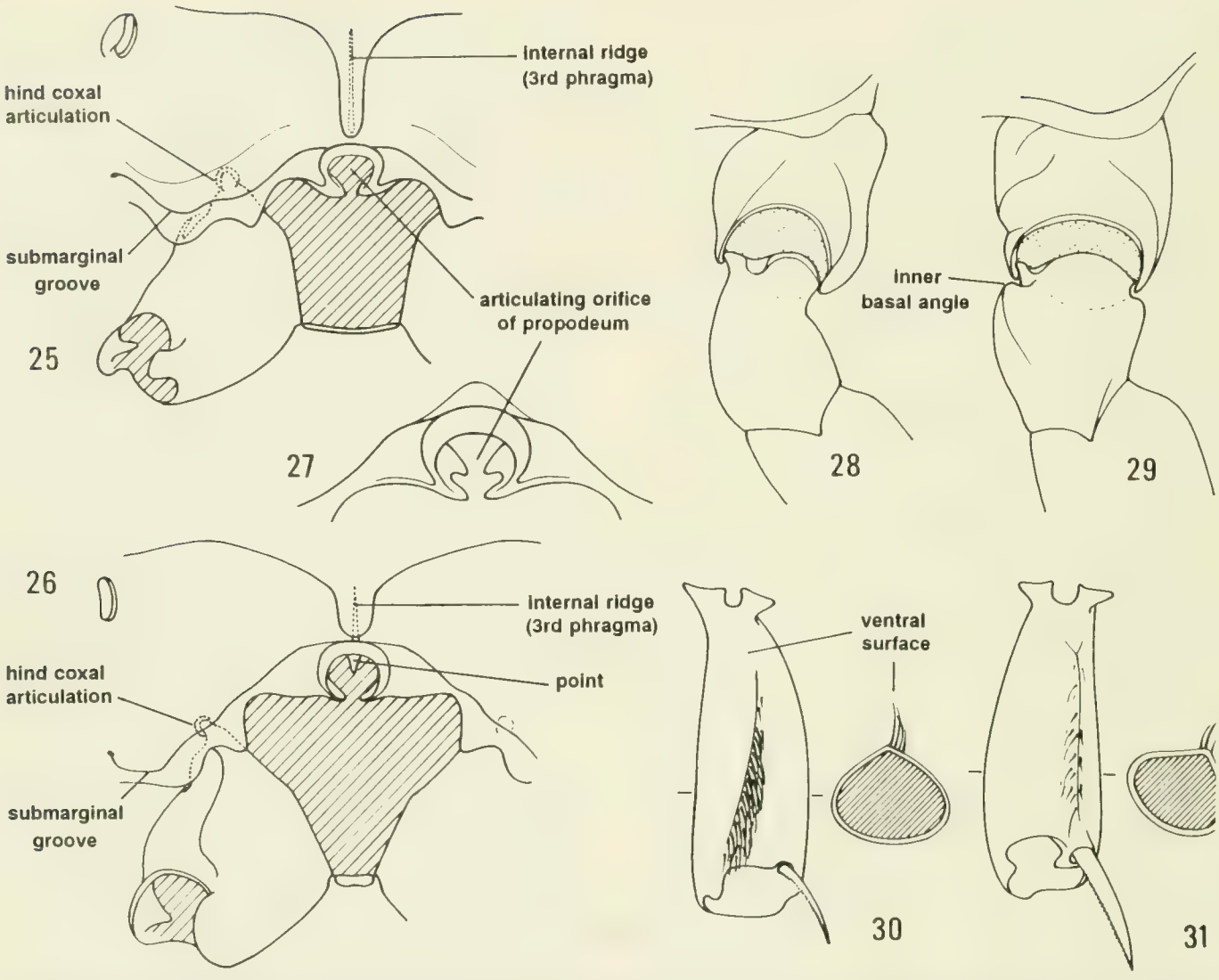


Fig. 25-31: 25. Propodeum, metapostnotum and hind coxa, posterior view, female, *Macropis steironematis*. **26.** Same, *Canephorula apiformis*. **27.** Articular region only, *Habropoda laboriosa*. **28.** Right hind coxa and trochanter, of *Anthidium porterae*, female, viewed from above. **29.** Same, of *Svastra obliqua*. **30.** Right middle tibia, of *Macropis steironematis*, female, ventral view and cross section near apical third. **31.** Same, of *Melissodes agilis*.

pendently and perhaps even by different means. In most cases it is by loss of the second transverse cubital but in some, the first transverse cubital may be lost. If this is true, of course there are two characters with identical plesiomorphic states, because loss of one vein is not homologous to loss of another.

101. Wing vestiture: (0) Hairy throughout. (1) Partly bare.

102. Length of marginal cell of forewing: (0) Equal to or longer than distance from its apex to wing tip. (1) Shorter than distance from its apex to wing tip.

103. Apex of marginal cell of forewing: (0) Pointed, on wing margin. (1) Separated from wing margin, pointed. (2) Separated from wing margin, rounded. (3) Open or closed by weak vein. State (3) is found only in Meliponini. Although variable in Melittidae, State (0) is the principal one found in that family and in other S-T bees and, being commonly associated with other plesiomorphic characters such as a large stigma, is considered plesiomorphic.

104. Stigma of forewing: (0) Longer than broad, length beyond vein r at least half as long as margin basal to vein r, margin within marginal cell convex or sometimes straight. (1) Longer than broad, length beyond vein r less than half as long as part basal to vein r, margin within marginal cell concave. (2) Small, about as long as broad to nearly absent. (3) Narrow, almost parallel-sided, as in *Apis*. State (0) is the usual condition in S-T bees; the exceptions are seemingly derived taxa like the Diphaglossinae and *Colletes* (Colletidae).

105. Jugal lobe of hind wing: (0) Long, 0.5 times length of vannal lobe (measured from wing base) or more. (1) Short, 0.26 to 0.49 times length of vannal lobe. (2) Shorter, 0.25 times length of vannal lobe or less. (3) Absent. In S-T bees the jugal lobe is long, e.g., 0.75 times length of vannal lobe or more. State (0) is therefore considered plesiomorphic even though the character is variable in the Melittidae.

106. Vein cu-v of hind wing: (0) Shorter than second abscissa of vein M, transverse or slanting. (1) About as long as second abscissa of vein M, slanting. (2) Over twice as long as second abscissa of vein M, slanting.

107. Gradulus of T2: (0) Directed backward above and behind spiracle. (1) Directed toward or reaching spiracle. (2) Absent.

108. Base of T2: (0) Without phragma-like apodeme. (1) With transverse, phragmalike apodeme. State (1) occurs in certain Xylocopinae and *Lithurge*.

109. Gradulus of S2: (0) Straight across medially or slightly curved posteriorly in middle. (1) Bisinuate, i.e., with two posteriorly convex curves. (2) Absent. Although most Melittidae have State (2), *Hesperapis* shows State (0) as do most other S-T bees.

110. Metasomal sternal scopa (female): (0) Absent. (1) Present. State (1) is principally a character of Megachilidae but certain oil-collecting bees (e.g., *Ctenoplectra, Tapinotaspis*) were also coded (1) although the sternal hairs function in gathering oil rather than pollen and probably evolved independently from those of megachilids.

111. Apex of S6 of female: (0) Entire or gently bilobed. (1) Emarginate, with lateral projecting lobes (Roig-Alsina, 1991, Figs. 11-13). State (1) is found only in Nomadinae.

112. Apex of S6 of female: (0) Without specialized coarse setae. (1) With groups of spinelike setae (Roig-Alsina, 1991, Figs. 3-10). State (1) is found in Nomadinae and Isepeolini.

113. Surface of T5 of female: (0) With prepygidial fimbria, hairs denser and longer than in hair bands of preceding terga. (1) Without prepygidial fimbria, i.e., similar to preceding terga.

114. Apex of T5 of female: (0) With polished margin of tergum absent or narrow and parallel-sided. (1) With broad, bare, polished margin wider in middle, margined basally by long, stiff setae.

115. T5 of female: (0) Without pseudopygidial area. (1) With pseudopygidial area. State (1) requires State (1) of Character 113.

116. Pygidial plate of T6 of female: (0) Present. (1) Absent.

117. T6 of female: (0) Not papillate. (1) Papillate or minutely roughened, dorsal surface hairless. State (1) is found only in the Fideliinae. In *Neofidelia* and *Parafidelia* the papillate area is the enlarged pygidial plate; this is probably also true for *Pararhophites*.

118. Pygidial plate of T7 of male: (0) Present, distinct. (1) Absent, but sclerotized apical rim suggests apex of plate. (2) Absent, without apical rim. This character varies among melittids but the presence of a pygidial plate is so widespread among other S-T bees that it is probably plesiomorphic. An alternative case, however, can be made for the repeated origin of this plate in males. Most females have a plate on T6; in both sexes it is on the last exposed tergum. The presence of the plate is clearly the plesiomorphic state in females (Character 116); it has a function in nest construction. Probably it is functionless in males. It might appear in males simply as a result of a regulatory change, which could occur independently in different lineages.

119. Apex of T7 of male: (0) Entire. (1) With two conical points.

120. S7 of male: (0) With two or four apical lobes. (1) Without apical lobes. (2) Short and transverse, without lobes. (3) Disc to whole sternum membranous.

121. S8 of male: (0) With single apical projection and moderate basolateral arms. (1) Without apical projection. (2) Bilobed apically. (3) Almost completely absent (in Meliponinae).

122. Gonobase: (0) Forming a complete ring. (1) Not evident ventrally (absent or possibly fused to gonocoxites). (2) Almost absent.

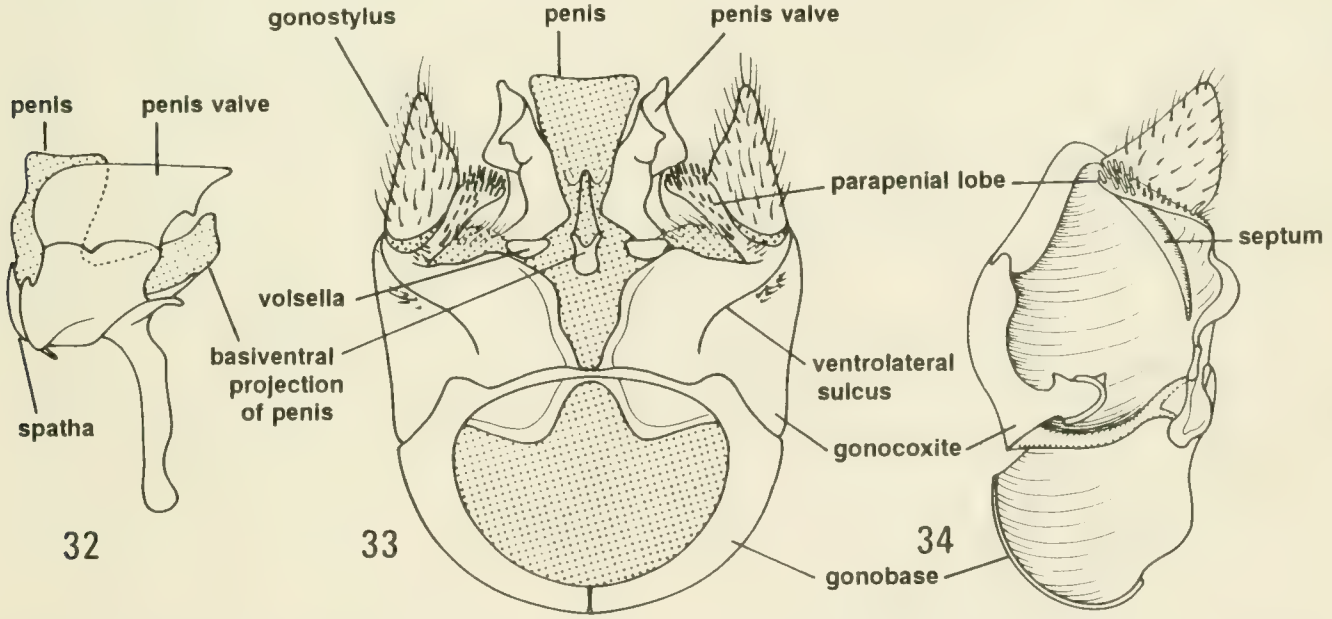
123. Gonocoxite: (0) Without sulcus or septum. (1) With ventrolateral oblique sulcus but no septum. (2) With septum, represented externally by sulcus, separating basal and apical parts of gonocoxite (Figs. 33, 34).

124. Ventral parapenial lobe of gonocoxite: (0) Absent. (1) Present, without strong setae. (2) Present, with strong, often peglike setae (Figs. 33, 34). This lobe is the ventroapical plate of Allodapini (Michener, 1975).

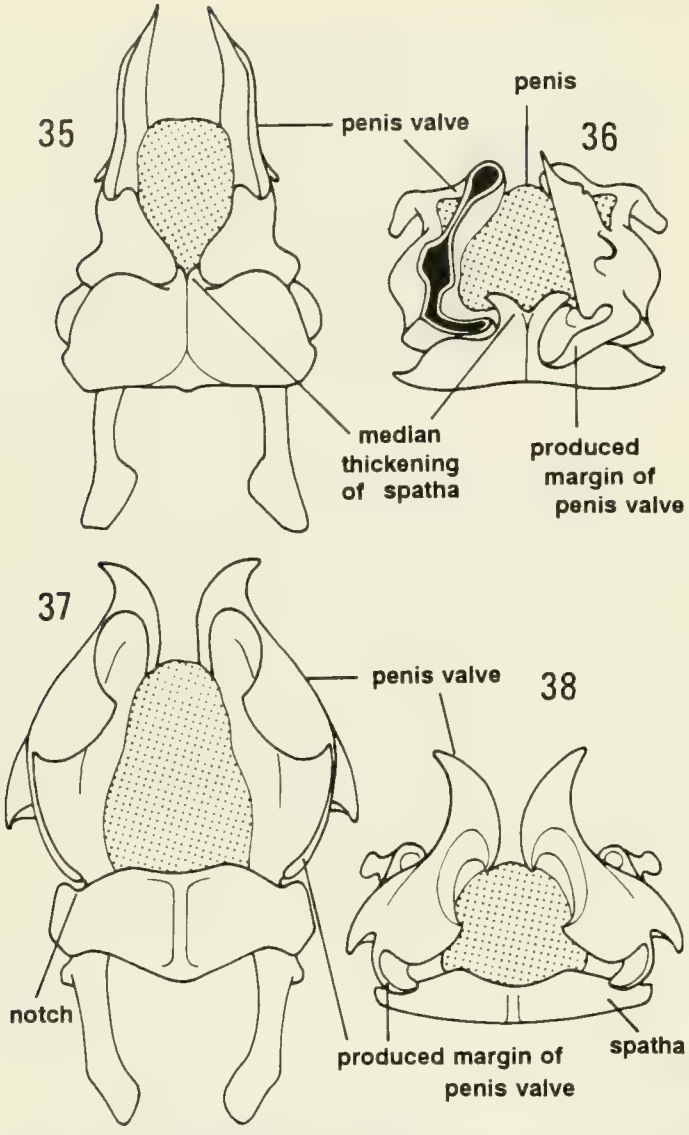
125. Gonostylus: (0) Articulated to gonocoxite although often with partial fusion (Fig. 33). (1) More or less indistinguishably fused to gonostylus (or absent?), the resulting structure being called gonoforceps. (2) Double, there being two nearly independent gonostylar structures arising from gonocoxite. This character is variable (0 or 1) among melittids and other S-T bees. The decision as to polarization is based largely on the morphological viewpoint that articulation must be primitive in insects.

126. Volsella: (0) Distinct, chelate. (1) A free sclerite but not chelate (Fig. 33). (2) Absent or fused to gonocoxite. The (0) state is as in most melittids as well as many other S-T bees.

127. Dorsal bridge of penis valves: (0) Short, not extended behind level of apodemes, or absent. (1) Expanded posteriorly as spatha (Figs. 35, 37).



Figs. 32-34. *Hexepeolus rhodogyne,* male genitalia. **32.** Penis and penis valve, lateral view. **33.** Genital capsule, ventral view. **34.** Internal view of right half of genital capsule, muscles removed to show septum.



Figs. 35-38. Penis valves and penis. **35.** *Tapinotaspis tucumana*, dorsal view. **36.** *Tapinotaspis tucumana*, apical view; one penis valve sectioned to show fit of its produced margin with median thickening of spatha. **37.** *Peponapis fervens*, dorsal view. **38.** *Peponapis fervens*, apical view.

128. Dorsal bridge of penis valves or spatha: (0) Lacking notches into which fit dorsal basal produced margins of penis valves. (1) Distal margin (of spatha) with two notches into which fit produced basal margins of penis valves (Figs. 37, 38). (2) Ventral surface of spatha with median thickening, lateral margin of which overhangs to form space into which fits produced basal margin of penis valve (Figs. 35, 36).

129. Penis with basiventral membranous projection: (0) Absent. (1) Present (Figs. 32, 33).

130. Base of gonostylus: (0) Not extending basad. (1) Extending basad on inner surface of gonocoxite. State (1) is found only in Tetrapediini.

131. Number of ovarian follicles or testicular tubules: (0) Three. (1) Four. (2) Five or more. Not many melittids have been examined for this character, but all S-T bees studied have State (0). State (2) is found only in some parasitic bees which have 5 to 13 and in *Apis*, which is very different, with 2 to 12 in workers, over 150 in queens.

Table 2 shows the states of the adult characters for the species listed in Table 1.

SELECTION AND CODING OF CHARACTERS OF MATURE LARVAE

The characters that we analyzed are those listed by McGinley (1981) that varied among L-T bees, and for which the plesiomorphic state was identifiable. Some were listed by McGinley (1981, Table 2) as "Cladistic Characters"; for others we believe the polarity is clear for L-T bees even though McGinley did not consider it clear for bees as a whole. For a few that McGinley considered "Cladistic Characters," we found polarity dubious for L-T bees; we excluded them from our list of characters. As with adult characters, plesiomorphic states were recognized usually using melittids as an outgroup. If there was variation among melittids, however, other S-T bees (colletids, andrenids) were used as a secondary outgroup. Moreover, if the other S-T bees differed as a whole from melittids, we concluded that the melittids probably had a family-level apomorphy, and considered that the other S-T bees exhibited the plesiomorphic condition for our study. Our judgment as to the plesiomorphic state sometimes differed from McGinley's because our outgroups are different; he dealt with bees as a whole while we are concerned with L-T bees. In some cases there are reasons to doubt our decisions as to polarity; these are indicated in the list of characters and in the following paragraphs.

As discussed by Michener (1953), various characters of bee larvae seem to have more primitive states in most L-T bees than in most S-T bees, even though the reverse is true for various adult characters. That is, in L-T bees the states of such characters are more like structures found in more ancestral Hymenoptera or other insects. Examples are Characters 1 (setae on the head capsule) and 20 (size of the antennal papilla). In both cases, the better developed state (longer setae, slender projecting papilla) is no doubt plesiomorphic for Hymenoptera as a whole. The reverse may be true for aculeate Hymenoptera, since they presumably evolved from parasitoids (Whitfield, 1992) in which larval structures are greatly reduced. Be this as it may, all Melittidae except *Meganomia* have reduced head setae and moderately developed to absent antennal papillae. Since *Meganomia* has many derived adult features (Michener, 1981), it is unlikely to exhibit the basic melittid larval structure and we therefore regard the remaining members of the Melittidae as good indicators of the plesiomorphic states for the analysis of the L-T bees. We therefore coded reduced head setae and reduced antennal papillae as (0); that is, among L-T bees, development of longer setae and antennal papillae is derived. Character 48 (labial palpal length) is similar except that the deviant melittid is *Macropis*, also a melittid with many derived adult features. In all these cases most S-T bees exhibit the character state that we have coded as (0). Of course a frequent state is not necessarily ple-

Table 2. Matrix of Character States for Adults
The characters and states are explained in the Annotated List of Adult Characters.

```
                  1234567891111111111222222222233333333334444444444555555555566666666667777777777888888888999999999911111111111111111111111111111
                            01234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012333
                                                                                                                                    01234567890123456789012345678901
Ancestor  00000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000
Eremapis  00211101000002000002002000101100011000111001001101120010000000001000000110001000000001010000000001010000001000000200010102100?
Teratogn  00201101000002000002002000101100011000011100100110112001010000000001000000110001200000002010002100000010000000000000010001012100?
Isomalop  00201101000001001002002000101100011000011100100110112001000010000010100001100102000000201000210000101000000000000001011101021000?
Exomalop  00201001000000000001012000101100011000011100100110112001000010000010100001100102000000201000210000101000000000000001002101021000?
Tapinota  00201001000002000002111000101101011000011100100110112001010001100001011110200010210000021100011000001120000100000000002101021200?
Tapinorh  00001001000002000002102000101101011000011100101110112001010001100001011110210010210000021100011000001010000000000000002101021200?
Arhysoce  00101101000002000002102000101101011000011100100110112001010001100002011110210010210000021100021000002010000000000002002101021200?
Paratetr  00111101000002000002002000101101011000011100100110112011010001100002011111210010200000001100002100000201000000000000002002101021200?
Monoeca   00101001000002000002202000101100011000011100100110112001010001100001010111010010000001121121000002010000000000000001210102102?
Caenonom  00101001000002000002202000101101011000011100100110121110000010000021121102100102100000021010001010000202010000000000000002101021200?
Ancylosc  00111101011002010002202000101100011000011100101110112001010001100001011011210000100000020100001000001000000000000000002002101121000?
Melitoma  00101101001001010002202100101101111001?111001001001120010100010000011012011210010200000020100001000001000000000000002102101021200?
Diadasia  00101101001002010002002000101101111000011100101100112001010001000011012010210010200000002010000000001000000000000002102101021200?
Diadasin  00101101001002010002002000101101111001?111101011101120010000010000011011011210012000000001010000000001000000000000002102101021200?
Ptilothr  00001101001002010002002000101101111001?111101011001120010100010000011012011210011200000001010000000001000000000000002102101021200?
Tetraped  00000110100001000002011000101100011100111001001011120010000010000010120102100100120000002110011010000102010000000000002110100120001?
Coelioxo  00001101001000010021011000100100?110001111101001011200100000100000301201021001000100000221100010100001020?000010000211000021000?
Tarsalia  00?01001010002000002202000101100011000111011001111120110000011000?1?100002?1?01010000000201000110000002210001?000000000210011202100?
Eucerino  00101001010102?00000?202000101100011000011100100101112101010001?00?1?100002?1?01020000000211000110000001010?000000000200210202100?
Canephor  01111001010101010002102000101100010110011100100101112001020001000010000102100100001000211000011100101200000000000000001020211002
Eucera    00111001010101000002202000101100011010011100101011112101020001100001010010210010200000002210001100001021000100000000000001020211001
Melissod  00111001010101000002202000101100011000011100100101112101020001100001010010210010200000002210001100000221000100000000000021020211001
Svastra   00111001010101000002202000101100011010011100101011112101020001100001011010210010200000002110001100000121000100000000000001020210001
Peponapi  00111101010101010002202000101100011010111100101101112101020001100001111010210010200000002210000100000121000100000000000021020211001
Anthopho  00101101000000000002202000111100011000021011001101122001000000010020000011311010000000021000020000112211000000000002110100020001
Habropod  00101101000000001002202000111100011000002100100101110?010000001000200001131101000000002100002000010211100000000000020101002200001
Deltopti  11101101000000000022021001110001100000210010010111211100000010001000011310100000000220000020000102110000000000002110101210000?
Centris   00001001000000000002001000101100011000001101100101112101000001010001000110310100000000220000020000102110000000000002110101221000?
Epichari  00001101000001000002102000101100011100001101100101122101000001010001000110210100000000221000020000102110000000000002101212110000?
Xeromele  00001101000001000002202000101100000000112100100101110010100000000010000112100112001000010100001000112112000000011000211102110001
Zacosmia  00001101000000000002212000100000?110001121001001011110101000000003000011210001200100001010000010011211200000011000001120010000?
Thyreus   00001111000000000002212000101100?100001121001201011110101000001000220001221001120010000001000010100112112000000110000211020121010001
Ericroci  00001101010000000012002000100100?101000121101001011121011000000100100001121000100010000002000000001111222020001000021111210200002
Mesonych  00001101010001000012012000101000010000121101001011121011000000010010001121220010001000000020001000011212220200010000211112101000?
Mesoplia  00001101010000000012012000101000111001121101001011121011000000010010001121000010001000000020001000011212220200010000211112102000?
Rhathymu  00001101010001000012002000100100?110001111111101011111010000000010010000112100110001000000100021000002021000000100021101112210002
Parepeol  00001101000001000002111010101100011000011100101001120010000000000020010102100010001000000010000010000020200000001100000101212110000?
Ecclitod  00001101000000010002102010100100011000011100101001120010000000000030010102?000010001000000010000010000020200000001100000101212110000?
Osiris    00011101000000000001201201010110001100011110010010011200100000000000200001031000100010000001000001000000200000001100020111000110000?
Lasiopodu 00001101000000000012002000100100011001?111001011001120010000001000200001021001100010000101000000000010100000010100201110012000?
Isepeolu  00001101000000000012202000100100011000011100100101112001000000100000001121000100010000021000000000111010000001001010110000110000?
Melectoi  00001101000000000012202000100000011000111100100101112001000000100100001021000100010000121000000000101010000001100101010000110000?
Neolarra  00001101000000000010201000010000001100101111001001101110010000000000200000210001000100000010000000111?020000101000000101220110102
Caenopro  00000111000000010002010000100000011000111111001001001110010000000000000113100010001000000000000001001020100010100002111001200002
Oreopasi  01011111000000110002010000100000011000011100120100111001000000000000000210210011000100000010000000100102010001010001100002000002
Triepeol  00011101000000000002110001000000100001121001001011010010000000000020000112100110001000000000000000020200000111010000101000100102
Epeolus   00011101000000000002100001000000100001121001001011010010000000000000100001131000100010000001000000000020200000111010000101100200102
Rhoqepeo  00011101000000000002110001000000100001121001001011020010000000000020000112100110001000000100000000020200000111010000101210110007?
Holcopas  00001111000000000010201000010000011000111001001001010010000000000020000113100010001000000010000000020200000111010000101210110007?
Brachyno  00001101000000110102010000100000011000111001001001010010000000000020000112100110001000000100000000020200000111010000101212110000?
Kelita    00001101000000001010201000010000011000111100100101112001000000000020100002101100010000010000000000020000011101000010222110102
Pachynom  00011001000000110102010000100000011000011100100110101001000000000020000110100010001000000000000020000011010000101220110000?
Centrias  00011101000000110112010000100000011000111001001101000010000000000020000110100010001000000100000000020100001101000101100210002
Biastes   00001101000000011102010000100000011000011100100100010000000010003000010210001000100000010000000010020200001110110001002201010?
Hexepeol  00001101000000001020100000100000011000012110102010010010000000000010000102100010000000001000000000020200001110100011022011010?
Manuelia  00001000010000110010100001010000110001111001001011200100000001000100001011001000000001010000000001020100001000020201010200?
Xylocopa  00001000010001000000010100101001010000110110100100112111000000000010000102100110000000010100002010012100000001000020211001210001
Ceratina  01001001010000110002010100101100011000111001001001120010010000010001000000021000120000000010000000000020101100001001020211001210001
Macrogal  01001001010000110002?000100100000010100111100100100112001001000010001100000021000100000000010000000010020001100001001020211010210?
Braunsap  01001101010000110002010100100000111001111001011001120010010000010001100000021000100010000001000000010000001100001001020211020210001
Bombus    00000101000001001002002000101000011000101111010111220010001001000010011210101120011111011000210100002130000000100102010001110001
Apis      00000001000001011002012000010000110001?011101201002200010011010210100012101111??211111011000210000023002000001001020132000210000
Melipona  00000001000001011002012000010000110000111012010112200010001101121010011120100111??211111011000010002003300100000100102013200021000?
Partamon  01000001000002?011002012000100100?110000011101201002200010001101121010001120100111??211111011100001002003010100000100102013200021000?
Euglossa  01011101000001?000002201010011100001101100101112111000101000011010122101112101111111100021010002220000000100102010100011000?
Eufriese  01011101010001?001002201100101100?110000011011001011121110001001000011010122101112101111101110021010002300000001001020101000110000?
Pararhop  00000000100000010000002000100000011100001101001011201100000100000300000021001100110000001100000001101000000100110111010000100000?
Neofidel  00101011100000000000001000101000010000102100100100112001000001000000000010212000100110000001100000000101100001001100100000000000?
Parafide  00100000100000010000207100010000001011027201011010112001000001170027??100117?701100110000011200000001011000?010011001000000000?
Lithurge  10000010100001000001000010001001110010111010001012011001001000030100102100110000000001000001110010000101001000000110001200000?
Trachusa  10010011000000110000100001000100111001011001001001220010001011000030001121001100010000010001000010022001001001002011000020000?
Anthidiu  10000011000000110000100001010100111000011000100101100030000111100110000000100010010022101001001002012000002000000
Hoplitis  10010010100000110000000000100010011100101100100100122001000101000030000001100010001000000100000011002120100100100201010001000?
Osmia     10010010100000100000010000100010011100101111010010011220010001011010030000111100010001000021000000111002110100100100201030000110000
Megachil  10010011100000100000010000100010011100101100100100122001000100000030000112100010001000001100000011100211010010010020300001200000
Coelioxy  10010011100000010000211000100010?111001011001001001220010001000000300001121000100010000010111000010000011100211000000100102030000120000
Ctenople  01001101000002000001201000101100010000101000000002001010001010010?021001001000010111000100101002000000100000020021000210000?
Macropis  00001000000000000000000001100000000000000100000000000??000000101000300000000000000000000000010000100010000000200000000000000000000
Melitta   00001000000000000000201001100000000000000100000000000??000000010003000010000000000000000000200000000000000000000000000000100000?
Dasypoda  00001000010000000000200001100000000000000100000000011000000001000310001000000000010000010000000010000100020000000020000000000?
Hesperap  00001000000000000000202000101000000000000100000000000??000000010003100010000000000000000000010000001000000000000000000000001000000
Meganomi  00001000000000000000202001100000000000000100000000000??000000010003100010200000000000000000000010000021000020000000000000001100000
```

siomorphic, but we believe that in these cases the plesiomorphic condition for L-T bees is widespread in S-T bees; any alternative negates the use of Melittidae as the closest outgroup and sister group of L-T bees.

For several other characters (43, 44, 46, 47, 49) the situation is less clear because there is less unanimity in the Melittidae, and melittids with more plesiomorphic character states such as *Melitta* sometimes have the more fully developed structures. However, since these characters are probably all functionally related in bees (in connection with cocoon spinning, see below), we believe that they have to be treated like Characters 1, 20, and 48, i.e., with the reduced condition being considered ancestral for L-T bees.

To summarize, other authors considered the better de-

veloped states of the characters listed above as ancestral and the reduced states as apomorphic. They were considering bees as a whole. For L-T bees only, we must reverse the polarity, in view of evidence from Melittidae, our first outgroup. In addition, if aculeates arose from parasitoids that show the reduced states, we believe that the polarity that we advocate for L-T bees may be appropriate for all bees. Reversions from the reduced states to more developed states may have occurred independently in various aculeate groups such as bees, sphecoid wasps, etc.

Most or all of the characters listed above may relate to cocoon spinning or the sensory apparatus needed for cocoon spinning. In L-T bees, taxa that do not spin cocoons, like the Nomadinae, Xylocopinae, and Anthophorini, have (secondarily) reduced states for these characters, although most L-T bees have the better developed states and spin cocoons. Most S-T bees do not spin cocoons and have the reduced states. However, it is obvious that developed states of these characters are not always associated with cocoon spinning. For example, many parasitoids spin cocoons although they have extremely reduced cephalic structures. Moreover, the cocoon-spinning S-T bees (Diphaglossinae in the Colletidae, Rophitinae in the Halictidae and some Melittidae) are equivocal in development of these structures; for example in the Diphaglossinae, antennal papillae are small, galeae are absent, but palpi are rather long.

One could argue that, if the above explanation is correct, one should list only a single character, rather than overweighting it with several manifestations thereof. However, none of the characters are perfectly correlated; each provides some different information. Given our present knowledge of insect development, it seems unwise to do more than note this situation. We suspect that many other characters are also not independent.

That cocoon spinning, involving silk production and spinning behavior, would evolve, after having once been lost, seems less likely than redevelopment of the individual structural features discussed above. There are therefore legitimate differences of opinion as to polarities. The subject deserves restudy by persons thoroughly familiar with bee larval characters.

ANNOTATED LIST OF LARVAL CHARACTERS

These characters are more fully explained by McGinley (1981). The number of each character is followed by McGinley's number in parentheses.

1 (1). Setae on head capsule: (0) Short and difficult to see. (1) Long and distinct. All melittids except *Meganomia*, which is probably a derived melittid, and many other S-T bees, have State (0), which we tentatively consider plesiomorphic for L-T bees, although presence of long setae must be plesiomorphic for aculeate Hymenoptera.

2 (2). Spiculation on dorsal surface of labrum: (0) Absent. (1) Present. Most melittids, all colletids and halictids, and some andrenids have State (0), which we tentatively consider plesiomorphic.

3 (3). Epipharyngeal spiculation: (0) Present. (1) Absent.

4 (4). Hypopharyngeal spiculation: (0) Present. (1) Absent.

5 (5). Dorsal and mesal maxillary spiculation: (0) Present. (1) Absent.

6 (6). Pigmentation of head: (0) Light. (1) Heavy. State (1) is known, among L-T bees, only in certain Nomadinae.

7 (9). Vertex: (0) Rounded. (1) Produced forward.

8 (10). Swelling above antennae: (0) Absent. (1) Present.

9 (14). Anterior tentorial pit: (0) High. (1) Low. McGinley's (1981) States 2 and 3 are lumped and coded (0); his State 1 is coded (1). All mellitids have State (0), as do most colletids and the genus *Andrena*. We therefore think that our polarity is appropriate for a study of L-T bees.

10 (15). Posterior tentorial pit: (0) At junction of hypostomal ridge and posterior thickening of head wall. (1) Anterior to or below this point. Among L-T bees, State (1) is found only in Nomadinae.

11 (16). Posterior thickening of head wall: (0) Well developed. (1) Weakly developed. (2) Absent medially.

12 (17). Median portion of posterior thickening of head wall: (0) Straight. (1) Curving forward.

13 (18). Posterior thickening of head wall: (0) Single. (1) Appearing double.

14 (19). Median longitudinal thickening of head wall: (0) Absent. (1) Developed only dorsally. (2) Extending forward to level of epistomal suture. Since nearly all colletids and andrenids have State (0), as do all melittids except *Meganomia*, which has State (1), and State (2) is found only in some L-T bees, we consider State (0) plesiomorphic. It is possible, however, that State (1) is plesiomorphic instead of State (0).

15 (20). Hypostomal ridge: (0) Well developed. (1) Weak.

16 (21). Hypostomal ridge: (0) Simple. (1) Divided posteriorly. State (1) is known only in certain megachilids.

17 (23). Angle of hypostomal ridge to posterior thickening of head wall: (0) Obtuse. (1) Perpendicular.

18 (24). Pleurostomal ridge: (0) Well developed. (1) Weak.

19 (26). Epistomal ridge or depression: (0) Well below level of antennae. (1) Arched upward to or above antennal level.

20 (30). Antennal papilla: (0) Enlarged basally and moderately developed to virtually absent. (1) Well developed, slender and projecting. Although it makes sense to believe that reduction of larval antennae might be a progressive process, all S-T bees except *Meganomia*, a derived melittid, have State (0), while many L-T bees have the better developed antenna of State (1).

21 (31). Number of antennal papillar sensilla: (0) 2-5. (1) More than 5. State (1) is found only in certain parasitic Anthophorinae.

22 (32). Clypeal length: (0) Moderate to long. (1) Short.

23 (33). Frontoclypeal area, in lateral view: (0) Not strongly produced. (1) Rounded, greatly produced. Among all bees, State (1) is found only in two nomadine genera and two melittid genera. [As elsewhere, this statement is based on McGinley's (1981) matrix; a third nomadine genus is now known to show State (1) (Rozen and McGinley, 1991).]

24 (34). Labrum in lateral view: (0) Moderately projecting beyond clypeus. (1) Strongly projecting. Among L-T bees State (1) is found only in Nomadinae.

25 (35). Labral tubercles: (0) Present, well defined. (1) Absent or poorly defined. This relates to the two rounded marginal tubercles. The pointed tubercles on the disc of the labrum found in Nomadinae are evidently not homologous (J. Rozen, in litt., 1993). Although melittids have State (1), State (0) is characteristic of nearly all andrenids, halictids and colletids and is therefore considered plesiomorphic; presumably State (1) is an apomorphy of melittids.

26 (39). Sensilla-bearing swellings on labral apex: (0) Present. (1) Absent. Because such swellings are present in most bees including our outgroups, we have reversed the polarity indicated by McGinley.

27 (40). Epipharynx: (0) Not produced. (1) Produced as distinct lobe. State (1) is found only in two genera of Nomadinae.

28 (44, 45). Mandibular spicules: (0) Absent or short. (1) Long and hairlike.

29 (47). Mandibular apex, ignoring teeth if present: (0) Acute. (1) Broadly rounded or truncate.

30 (48, 49). Mandibular apex: (0) Simple. (1) Bidentate with

dorsal tooth longer or teeth subequal. (2) Bidentate with ventral tooth longer. All colletids and most andrenids, halictids, and melittids have State (0), which we therefore consider ancestral. The polarity is tentative; given the multiple teeth of wasps, one would expect two teeth to be ancestral to one.

31 (51). Apical part of mandible: (0) Not attenuate. (1) Attenuate.

32 (52). Mandibular cusp: (0) Well or moderately defined and produced. (1) Weakly defined or absent.

33 (53). Cuspal projection of mandible: (0) Absent. (1) Present.

34 (54). Mandibular cusp: (0) Multidentate. (1) Smooth, edentate.

35 (55). Teeth on dorsal apical edge of mandible: (0) Present. (1) Absent.

36 (56). Ridge delimiting apical mandibular concavity: (0) Hidden from above by dorsal apical edge. (1) Visible from above, exceeding dorsal apical edge.

37 (57). Mandibular apical concavity: (0) Weakly to moderately developed. (1) Strongly developed.

38 (58). Mandibular concavity: (0) Oblique, not scooplike. (1) Scooplike.

39 (61). Labiomaxillary region: (0) Moderately recessed. (1) Produced. (2) Strongly recessed. All andrenids and many members of all other S-T families including half of the melittids have State (0), which is tentatively considered plesiomorphic for L-T bees. Our treatment here is similar to that of other characters that seem to be associated with cocoon spinning. (See sections on Selection and Coding of Characters of Mature Larvae.) McGinley (1981) and J. Rozen (in litt., 1993) regard State (1), produced, as ancestral but for the reasons indicated we suspect that the intermediate condition, State (0), is ancestral for this study.

40 (62). Labium and maxilla: (0) Distinct. (1) Fused.

41 (63). Labium: (0) Exceeded in length by maxilla. (1) Subequal to maxilla. (2) Exceeding maxilla.

42 (65). Inner apical maxillary surface: (0) Rounded. (1) Produced mesally. In all Andrenidae, nearly all colletids, and mellitids except *Dasypoda*, State (0) is found. We therefore have changed McGinley's polarization for the study of L-T bees.

43 (68, 69). Maxillary palpus: (0) Elongate, usually twice as long as basal diameter. (1) Apparently absent. (2) Shorter than basal diameter.

44 (70). Maxillary palpus: (0) Slender. (1) Robust. Since State (0) is found in all andrenids and many colletids, and in half the melittid genera listed by McGinley, it is tentatively regarded as plesiomorphic.

45 (71). Location of maxillary palpus on maxilla: (0) Apical. (1) Dorsal. (2) Ventral. State (0) characterizes all but one melittid and considerable numbers of colletids and andrenids. It is therefore tentatively regarded as plesiomorphic.

46 (72). Galea: (0) Absent. (1) Present. Nearly all S-T bees except three melittid genera lack the galea, while it is present in many L-T bees. See discussion in the section on selection and coding of larval characters.

47 (73). Labial division into prementum and postmentum: (0) Weak or absent. (1) Strong. All andrenids, nearly all halictids, and about half the colletids have State (0), which also occurs in the melittids *Hesperapis* and *Capicola*. We tentatively accept the polarity indicated. This character is largely associated with Character 39 and the same comments apply to both.

48 (76). Labial palpus: (0) Shorter than maxillary palpus. (1) Subequal to or longer than maxillary palpus. State (0) occurs in all andrenids, most colletids, and all but *Macropis* in the Melittidae. This state is therefore considered plesiomorphic for L-T bees.

49 (77). Salivary lips: (0) Greatly reduced or absent. (1) Well developed. Although variable in melittids, the presence of State (0) in all andrenids and nearly all colletids and halictids suggests the polarity indicated.

50 (79). Salivary opening: (0) Transverse. (1) Recurved. (2) Circular or oval. All the melittids have State (0). Other S-T bees mostly have states not represented among L-T bees, although some colletids have State (0).

51 (80). Salivary opening: (0) Nearly as broad as distance between labial palpi or broader. (1) Much narrower. Although melittids are variable, all andrenids and halictids and all colletids except *Colletes* have State (0), which is therefore considered plesiomorphic.

52 (81). Position of salivary opening on labium: (0) Apical. (1) Dorsal. State (1) is found only in Xylocopinae.

53 (84). Hypopharyngeal size: (0) Normal. (1) Enlarged. Among L-T bees, State (1) occurs only in certain parasitic bees.

54 (85). Apex of hypopharynx: (0) Rounded. (1) Bilobed. Although variable in melittids, this character is as State (0) in all halictids and andrenids and nearly all colletids.

55 (87). Hypophyrangeal groove: (0) Distinct. (1) Absent or indistinct.

56 (88). Body integument: (0) With patches or transverse rows of conspicuous spicules or setae. (1) Without conspicuous spicules or setae. Rozen (1987, p. 8) showed that this and the next character, as treated by McGinley (1981), require restatement. While constrained by the character states as recorded by McGinley, we have tried to word the characters in ways that remain meaningful for analysis. The "setae" of many megachilids are primarily elongate, erect spicules. A few true setae are intermixed, and are as long as the spicules. The hairy appearance of most megachilid larvae is a strong apomorphy (Character 57). Character 56 has to do with patches or rows of spicules and setae, mostly directed backward, not comparable to the generally distributed erect hairs found on many megachilids.

57 (89). Body integument: (0) Apparently nonsetose. (1) Seemingly conspicuously setose. Sphecids and most megachilids are conspicuously hairy, and as pointed out by McGinley (1981) and Michener (1953), this should be the plesiomorphic state. However, near absence of hairs in all S-T bees except certain melittids requires us to polarize this character as indicated above, implying a reversion in megachilids. Presence of hairs in most allodapine larvae shows that they can appear in lines that nearly lack them.

58 (92). Paired dorsal darkened areas on thoracic segments: (0) Absent. (1) Faintly evident.

59 (93). Body length: (0) Moderate. (1) Long.

60 (94). Body form: (0) Robust to moderately robust. (1) Slender.

61 (95). Body, as seen in side view: (0) Widest medially. (1) Widest posteriorly.

62 (101). Median dorsal abdominal tubercles: (0) Absent. (1) Present.

63 (102). Dorsal conical tubercles, two per segment, usually darkened and pointed, on thorax and at least first abdominal segment: (0) Absent. (1) Present.

64 (105). Venter of abdominal segment IX: (0) Not protuberant. (1) Protuberant.

65 (106). Length of abdominal segment X: (0) Moderate. (1) Long. (2) Short.

66 (109). Venter of abdominal segment X: (0) Rounded, not produced. (1) Produced. This character is sufficiently variable among S-T bees that the polarity has to be considered doubtful.

67 (111). Dorsum of abdominal segment X: (0) Without transverse line or ridge. (1) With transverse ridge. (2) With transverse line. This character varies in Melittidae but shows State (0) in all Andrenidae and nearly all Colletidae.

68 (113). Anus positioned: (0) Apically. (1) Dorsally. (2) Ventrally.

69 (116). Spiracular sclerites: (0) Absent. (1) Present.

70 (117). Spiracular atrial shape: (0) Subglobular to subquadrate to broad and rounded. (1) Very broad and shallow. Because State (0) occurs in all mellitids and andrenids as well as some colletids, we consider it plesiomorphic for L-T bees.

71 (118). Spiracular atrium: (0) Not or little produced above body surface. (1) Strongly produced. State (0) is found in almost all S-T bees except some melittids.

72 (119). Spiracular atrial wall: (0) Not ridged. (1) Ridged.

73 (120). Spiracular atrial wall: (0) Without spines. (1) With small spines or denticles. (2) With long spines. Spines or denticles are widespread and may be plesiomorphic for bees as a whole, but since all andrenids, nearly all melittids, and many colletids have State (0), we consider it plesiomorphic for this study.

74 (121). Spiracular atrial rim: (0) Present. (1) Absent.

75 (122). Width of spiracular peritreme: (0) Narrow (even absent) to moderate. (1) Very wide.

76 (125). Primary tracheal collar: (0) Smooth. (1) Spinose.

77 (126). Spiracular subatrial length: (0) Moderate, more than two to four times atrial length. (1) Over four times atrial length. (2) Twice atrial length or less. Although all melittids except *Meganomia* have State (0), variability in other S-T bees makes our polarity for this character inconclusive.

Table 3 shows the states of the larval characters for the species included in this study.

PHYLOGENETIC ANALYSES

Computer analyses of exemplar species using data in the character matrices (Tables 2 and 3) were made with Hennig86 1.5 (Farris, 1988) running on a Zenith 386. Certain analyses were also made with PAUP 3.0g (Swofford, 1990) using heuristic search with TBR branch swapping and the Deltran option. The results were identical to those obtained with Hennig86. Analyses that resulted in more than one tree were each summarized by a consensus tree using Hennig86.

Maddison (1991) has demonstrated that sometimes multiple islands of minimum-length trees exist and that not all of them are found in simple analyses. Therefore, using the trees produced by the algorithms h, h*, m, and m* provided by the Hennig86 program and two arbitrarily constructed trees, a multiple search for minimum-length trees was made applying the branch swapping algorithm bb*. For most analyses a single set of such trees was obtained, but in the study of larvae (Analysis E) two islands of trees were found.

In studying the cladograms, and seeing that a character state appears at two or more widely different places, it is tempting to re-examine the characters, discern differences between apparently distantly related possessors of a given state, and decide to make two or more characters, thus eliminating apparent convergence. We have done very little of this, although the result would have been cladograms with higher consistency indices. This sort of activity is likely to be highly subjective, because with the desire to improve the tree, one can often find differences between similar structures in different clades that can be interpreted as indications of independent origins. It seems better not to engage in such potentially circular activity except in the clearest cases. See also Concluding Remarks.

In the analyses presented below, we have not introduced differential weighting of characters. To do so *ad hoc* is arbitrary. We tried the successive weighting option of Hennig86 but as might be anticipated, it accentuated the predominance of correlated characters related to the parasitic way of life.

Within most of the analyses (A to H) the various minimum-length trees were similar to one another in the topology of larger units and to a considerable extent were fully resolved. We therefore selected a minimum-length tree for presentation of some of the analyses. When such trees differ, resulting in polytomies in consensus trees, the matter is mentioned below, as are the two islands of trees in Analysis E.

The following is a list of the analyses:

Analysis A was based on the full matrix (82 taxa, 131 characters) of adult characters. (See Table 1 for list of taxa, List of Adult Characters for character state codes, and Table 2 for the matrix.) Tree length (L) was 894, number of minimum-length trees (T) was 756, consistency index (ci) was 19, retention index (ri) was 65. One of these trees is shown as Cladograms 1a and 1b. After the first branch swapping a full buffer prevented further swapping. For this reason Analysis B was performed.

Analysis B was based on a matrix reduced in information content by collapsing to polytomies four groups, namely, Melittidae (Cladograms 1a, 1b, Node 2), Megachilinae (Node 7), Emphorina (node above 34), and Eucerini (node above 39). Collapsing was done by changing characters of taxa that varied within the group to the state found in the root of the group in Analysis A. When the state of a character in the root was equivocal it was not changed. Thus the matrix was the same size as for Analysis A but indicated much less diversity for the four groups listed. For Melittidae, character 73 was equivocal and character 100 was also not collapsed because to do so would have made two submarginal cells plesiomorphic, whereas we believe that three is the plesiomorphic condition. Other characters that were equivocal were, for Megachilinae, 79; for Emphorina, 21; and for Eucerini, 121. Statistics for Analysis B: L 762, T 270, ci 22, ri 70. There was no problem of a full buffer limiting swapping. No cladogram is provided to represent results of Analysis B because tree topologies were so similar to those of Analysis A.

Analysis C used the same modified matrix as for Analysis B, except that five characters (19, 29, 84, 105, and 113) that seem related to cleptoparasitism were omitted. The derived state of each of these characters is found only or largely among parasitic bees and the ancestral state among nonparasitic bees. This manipulation was made because in Analyses A and B, features characteristic of parasitic taxa appeared as ancestral for both parasitic and nonparasitic bees. We reject hypotheses that a nonparasitic bee could evolve from a parasitic ancestor, because of the parasites' loss of behavior and structures (like the pollen-carrying scopa) necessary for successful nest construction and provisioning. Statistics: L 719, T 176, ci 23, ri 70. The basal parts (i.e., to the tribal level but largely without genera) of one of the trees is shown as Cladogram 2a, and a simplified version in Cladogram 2b.

Analysis D used the matrix of Analysis A except that all cleptoparasitic taxa were omitted, resulting in 54 included taxa. Like Analysis C, this was an effort to determine whether the parasitic taxa were greatly influencing, because of convergence misinterpreted as homology, relationships shown among nonparasitic taxa. Statistics: L 628, T 1712 plus over-

Table 3. Matrix of Character States for Mature Larvae
The characters and states are explained in the Annotated List of Larval Characters.

```
          1234567891111111111222222222233333333334444444444555555555566666666667777777
                    0123456789012345678901234567890123456789012345678901234567890123456

Ancestor  0000000000000000000000000000000000000000000000000000000000000000000000000000000
Macropis  0100100000000000000000010000000000000102000011110000001000000000110000000000
Melitta   0100100000000000000000010000100000000102000011010000100000000000010001000000
Dasypoda  0000000000000000000000010000200000000001212010001000000000000000010001000000
Capicola  0000000000000000000000101000000000000000021000000100000000000000000000000000
Hesperap  0000000000000000000000101000000000000000021000001000001000000000000001000000
Meganomi  1000010000000100000100001000000000000102000011010000000100000000010000000002
Ctenople  1000100010000100001100001000110101101110210020111000010010000000001100000102
Stelis    1011100010010001001101001000020101001110110020111000010110011100200101012000 2
Lithurge  1011000010010101001001001000020011101110110000111010010010011000200000000200?2
Dioxys    1011100010010000101101001000021101000010210020111000010010011000000000001200?0
Hoplitis  1011100010010101001001001000020101101100010020111000010110001100000010010001001
Coelioxy  1011100010010000001101001000120101101010210020111000010110011100200100011000 2
Trachusa  1010100010010101001101001000100101101110110000111000010110011100200100002000 2
Megachil  1011100010010101001101001000020001101110110020111000010110011100200100012002?2
Osmia     1011100010010101001101001000020101100110110020111000010110011100200100012002?2
Anthidiu  1011100010110001011101001100020101000110210020111000010110011100200100010000?0
Dianthid  1011100010110000011101001100020101001110110020111000010110011100200100010000 0
Ashmeadi  1011100010110000011001001000020101100110120101000000110011000010001?00????2
Fidelia   1000000010000100007101001000120011101110210020111010010011000020110100100 2
Neofidel  1011100010010100101101001000020011101110210020111010010110011000201100001000 2
Parafide  1000001010000101101101001000120011101110210020111010010010011000201101001000 2
Pararhop  0011100010010101101000001100021111100110210020111010010000000000200100100010 1
Melecta   0000000000000100000110001000100000001100200020101000010100100000001100002000 2
Thyreus   0100000000000100100?00100001001011011002?002000001011110000000000001000021002
Zacosmia  0010100000000000000100001000000001101 12?200000111000?1?1000000000011000000002
Rhathymu  0000000100000100000010001000100101101102001201110001100010000200100002000 2
Acanthop  0010000010000100101010000000100101101110200100101000111001010000200100001000 2
Isepeolu  0010100010200000110010001000001101000010200000111000011100000000000000000100
Protepeo  1011000010100100010100001000000101001100110100111010001010000100001107?1??????
Triepeol  0000100001100110110000001000000000110002120212000021010100010000010001010100 2
Epeolus   0000100001100110110000001000000010110002120212000021010110000000000001010100 2
Nomada    0000110001201110010000010010000000000021200100000210101000000000000001000002
Oreopasi  0011100001201110111000000000000101000021200100000210101000000000100000020000
Pseudodi  0011110001200110111000010000000101000021102100000210101000010000000100002010 2
Ammobate  0011110001201110011000010010000101100021202120000210101000001000000000000002
Morgania  0011110001201110011000010000000101000021202100000210101000000000000001010200 0
Holcopas  0000100001200110010000010000000101000021202120000210101100010000000001000000
Neopasit  0011000001201110010000100000001101000021201??00?021000100000000120000000010 0 0
Neolarra  0011000001201110010000100000001101000021201??00?021000100000000110000000200 0 0
Xenoglos  1101000010000200000000000001010001111010110001111000000100000000000101002110 0
Peponapi  1101000010000200001000000000101000110101011000111100000010100000000001010021100
Melanoma  0000001101200010010000010000001101000021200020000210100010000000010100012000 2
Paranoma  0000001101200010010000000000001101000021200020000210100010000000010100112000 0
Centris   1001000000000100000000001000110101001110200001101010000011100000020010001010 0 0
Epichari  0000000000000100000000001000110100101100002101110010010110000000020010001100 1 0
Habropod  0011000000000100000000000001110101001100012100000110?010000000000010011200 1 0
Anthopho  0010000000000100000000000001001010011000121000001100001000000000001000120010
Diadasia  0000000000010200000100000000101100110100210020101000000010100010001201100000002
Melitoma  1010000000010200000100000001010001101010010020101000000010100100001100000002
Exomalop  1000000000000200000000001001010100000010210000101010000000000001000100000000
Xylocopa  1011000010010100010100001100010101001110112000100211001000010000000201001000 1
Ceratina  1011000010010100001000001000011101001010102001000211001100000000000000??????0?
Allodape  1011000010110110001100001000101101100020201??00?021100110000010011010??1???01
Paratetr  0000?000000020000000001000020100001110112?001110000100000000010011000000100
Apis      1110000000110110111000001000000101100010202021111000001100011000001001010110 1
Bombus    1010100010010200001000001000120101101110200000111000000010011010012101011100 1
Eufiesea  1000000000010100010100001100120101101110200001101000001010011010012101010020 1
Melipona  1110000010110010111000001001101101000110202101111000001000000010001101010100 1
Trigona   1110000010110000111000001000101101000?10202001101000001000000010001101010100 1
```

flow, ci 26, ri 66. The consensus tree based on the 1712 trees is shown as Cladogram 3a.

F. A. Silveira repeated our Analysis D and then re-examined the relationships using successive approximations character weighting (Farris, 1969). Statistics: L 635, T 8, ci 26, ri 66. The topology different from that of the first part of Analysis D is presented in Cladogram 3b.

Analysis E was based on the matrix of characters of mature larvae (61 taxa, 77 characters). See Table 3 for the matrix and taxa and the List of Larval Characters for characters and states. Two islands of trees were found. For the larger island, the statistics are: L 482, T 176, ci 18, ri 67. The consensus tree is shown as Cladogram 4. The smaller island resulted in 16 trees, and otherwise the same statistics. As noted below, the trees of the smaller island were not useful and no cladogram representing them is presented.

In order to compare analyses based upon larval and adult features, we reduced matrices to include only taxa for which both character sets were available, as follows:

Analysis F was based on larval characters (47 taxa, 77 characters). Statistics: L 411, T 12, ci 21, ri 63.

Analysis G was based on adult characters (47 taxa, 131 characters). Statistics: L 625, T 940, ci 27, ri 62.

Analysis H was based on a matrix (47 taxa, 208 characters) consisting of both larval and adult characters, i.e., matrices for Analyses F and G combined. The taxa are those in common at the genus level between Analyses A and E, except that larval *Allodape* and adult *Braunsapis* characters constitute one taxon for purposes of Analysis H. Likewise adult *Biastes* and larval *Neopasites* were associated, as were adult *Nomada (Pachynomada)* and larval *Nomada* (*Nomada* s. str.) Statistics: L 1079, T 1, ci 24, ri 60. The single tree, in summary form, is shown as Cladogram 5.

In Cladograms 1 and 2 certain nodes are numbered, 1-39 in Cladograms 1a and 1b and 40-59 in Cladograms 2a and 2b.

Analysis A: Of the trees derived from Analysis A, we present one (Cladogram 1a) in full detail because it is based on all the taxa and all the characters. As will be shown below, other analyses provide better phylogenetic hypotheses.

A striking feature of Cladograms 1a and 1b is the extensive resolution. The consensus tree (Cladogram 1b) shows few polytomies; that is, most of the topological features of Cladogram 1a are found in all the trees based on Analysis A. The polytomies in the consensus tree (which in all other respects, of course, is like Cladogram 1a in topology) are listed below; the genera included in the family-group taxa are listed in the section on Classificatory Results.

1. Within the Melitidae (Node 2), four groups form a polytomy: *Macropis, Dasypoda, Hesperapis,* and a common stem for *Melitta* and *Meganomia.*

2. Within the Megachilinae (above Node 7), a polytomy supports four branches: *Osmia, Hoplitis,* the Megachilini and the Anthidiini.

3. *Isomalopsis, Exomalopsis,* and the stem leading to all taxa above (Node 31) form a trichotomy. (See reanalysis by Silveira, 1993.)

4. Immediately above this trichotomy there is another consisting of *Ctenoplectra,* the Emphorini, and the (Eucerini + *Tarsalia*) + the Tapinotaspini (Nodes 33, etc.).

5. Within the Emphorini (node above 34) there is a trichotomy consisting of *Melitoma, Diadasia,* and *Diadasina* + *Ptilothrix.*

6. Within the Tapinotaspini (Node 37) there is a polytomy consisting of *Caenonomada, Monoeca, Paratetrapedia* + the subgenus *Arhysoceble,* and *Tapinotaspis* + the subgenus *Tapinorhina.*

7. *Eucerinoda,* the rest of the Eucerini, and *Tarsalia* (Ancylini) form a trichotomy (Node 38).

8. Within the subtribe Eucerina (node above 39) there is a trichotomy consisting of *Canephorula, Melissodes* + *Svastra,* and *Eucera* + *Peponapis.*

Items 3 and 4 in the above list are the only ones involving stems leading to other major taxa.

There are few uniquely derived characters supporting the major (lower) nodes of Cladogram 1; a strong exception is Character 131 (number of ovarioles or testicular tubules) in Node 5. It is not surprising that some of the nodes, especially those supported by few characters (e.g., 9, 17, 19, 27), are weak and for biological understanding should be collapsed on the basis of our study. Further study by Silveira (1993), however, supports some of these nodes.

The characters of Node 1 (the common stem) include two apomorphies of melittids and L-T bees together (27-1, 42-1). A discussion of these and other common characters of Melittidae and L-T bees was given by Michener and Greenberg, 1980. Characters 68-3 (pre-episternal ridge) and 100-1 (submarginal cells) are reductions that are reversed at various points on the tree. We do not believe that they represent the true course of evolution because regaining of lost structures (e.g., a wing vein, character 100) is unlikely. See subsequent analyses for discussion.

Characters of Node 3 include several features of the mouthparts (34-1, 35-1, 41-1, 45-1, 48-1, 51-1, 52-1, 53-2 and 56-1) that are characteristic of L-T bees and differentiate them from S-T bees. Although the node is strongly supported, for most of these characters there are scattered reversals, and all but 56 reverse at least once. *Ctenoplectra* is the only taxon that reverses several (seven of nine) of these characters, including 48-1 which is the hallmark of L-T bees. Characters 76-1 (hind coxal articulation) and 91-1 (shape of middle tibia of female) are also features of most L-T bees, with only one reversal *(Tapinotaspis)* for 76 and scattered reversals for 91. Characters 84-1 (basitibial plates) and 113-1 (prepygidial fimbria) represent losses at Node 3; the structures reappear again elsewhere on the tree. Regaining of lost structures is not evolutionarily likely.

Node 5 is strongly supported by character 40-1, which is reversed only in Node 23. Character 122-1 is reversed only within Nomadinae and in *Coelioxoides* and *Isepeolus.* Character 131-1, four ovarioles or testicular tubules instead of three as in Megachilidae and S-T bees, does not reverse although more than four (131-2) occur in most Nomadinae, in *Ericrocis* and in *Apis.* Character 105-2, a very short jugal lobe,

is primarily a feature of parasitic bees. In the cladogram it is reversed in Nodes 19 and 21. We do not believe this represents a likely evolutionary pattern, although we know nothing of the function of the jugal lobe or why it should be small in parasitic bees. Character 126-2 (volsella) is a loss. The volsella reappears in Node 21, in the Osirini, in the Isepeolini, in *Coelioxoides*, and in some Nomadinae. Since reacquisition of a lost structure is improbable, we question the probability of this reappearance.

Node 7 (Megachilinae) is supported by Characters 1-1 (subantennal sutures) and 31-1 (dististipital process), found only in this subfamily, although neither is conspicuous or uniformly well developed. Character 7-1 (long labrum) appears also in *Neofidelia*, *Thyreus*, and some Nomadinae, although in the Apidae with a long labrum, it does not have the broad basal articulation to the clypeus found in Megachilinae, and is clearly independently evolved.

Node 8 (Nomadinae) is supported by Character 53-1, which represents reduction of the flabellum as is frequent in parasitic (and some other) taxa. Character 111-1 (shape of S6 of female) is unique for the Nomadinae. Character 131-2 (more than four follicles) occurs in all Nomadinae for which the character is known except some species of *Nomada*. The clades within the Nomadinae are considered in the discussion of Classificatory Results.

Node 9 is supported by Characters 23-2 and 30-1, which are reversed in scattered taxa. Character 127-1 (spatha present) should probably be in Node 5 since most Nomadinae that do not have reduced genitalia have a spatha. The spatha is lost in scattered taxa above Node 9.

Node 17 is best supported by Character 68-1 (pre-episternal internal ridge curving back to scrobe), but the ridge is reduced or lost in various taxa (mostly parasitic) and extends a short distance downward (68-0) in *Isepeolus*. This node is not strongly supported.

Most of the remaining numbered nodes, likewise, are supported principally by characters that are weak because of repeated reversals and appearance of the same states also elsewhere in the tree. The following are the node numbers, each followed by a dash and numbers of character states that are infrequently reversed or repeated elsewhere in the study and therefore appear to give the stronger support for each: 18–50-1, 79-1; 19–89-1; 20–54-1, 74-1; 21–104-1; 23–90-1, reversal 40-0; 24–101-1, reversals 80-0, 91-0; 26–reversals 5-0, 75-0; 30–89-2; 31–62-1, 70-1, 79-1, 121-2, reversal 80-0; 33–58-1; 35-90-1; 36–63-1, reversal 6-0; 37–32-1, 72-1. Particularly weak nodes are 17, 18, 19, 21, 27, 30, 32, and 35.

The following are comments on strengths or weaknesses of the other numbered nodes.

Node 22 is supported especially by Character 106-2 (long, oblique vein cu-v of hind wing), which is found only here, although a less extreme version (106-1) occurs in some Anthophorini and in *Rhathymus*. Character 41-2 also appears in Anthophorini. Character 101-1 also appears in Anthophorini and elsewhere. Character 102-1 also appears in *Anthophora* and *Centris*, as well as elsewhere. Character 123-2 occurs also in *Epicharis*, some Osirini, and some Nomadinae. None of these characters seems related to the parasitism of the Ericrocidini and Melectini.

Node 25 (the apine clade) is one of the best-supported nodes in the study. Character 60-1 (expanded pollex) is unique except for the very different sort of expansion in Megachilinae. Character 85-1 (tibial corbicula) occurs elsewhere only in *Canephorula*. Other characters having to do with pollen manipulation and transport, Characters 86-1, 87-1, and 88-1, are unique to this node except that 87-1 occurs also in *Ctenoplectra* and 88-1 is reversed in Meliponini. Character 74-2 occurs also in some Melectini and Ericrocidini. Character 78-1, otherwise unknown in L-T bees, is reversed in Meliponini. Thus this node is supported not only by the well-known hind tibial characters but also by other features. Character 105-3 (loss of the jugal lobe), however, is reversed to 105-0 in *Apis* and Meliponini. Reappearance of lost structures is improbable and this reversal is evolutionarily unlikely; independent losses in Euglossini and *Bombus* involve the same number of steps as one loss and one gain and would be more likely.

Node 27 seems supported by Character 29-1 (stipital comb). This character, however, appears also at Node 23 and in most Osirini. Moreover, some Nomadinae have stipital concavities; they are probably derived from ancestors with the comb. Probably 29-1 should be at Node 5, as a character of Apidae, lost in numerous parasitic taxa. If this were done, Node 27 would have little support.

Node 28 has four reversals (6-0, 8-0, 23-0, and 30-0) of characters that appeared in Nodes 5 and 9. This supports the movement of the Xylocopinae toward the base of the tree as in Cladograms 2, 3, and 5, eliminating the reversals. Character 120-2 is found elsewhere only in *Apis*, where it looks very different.

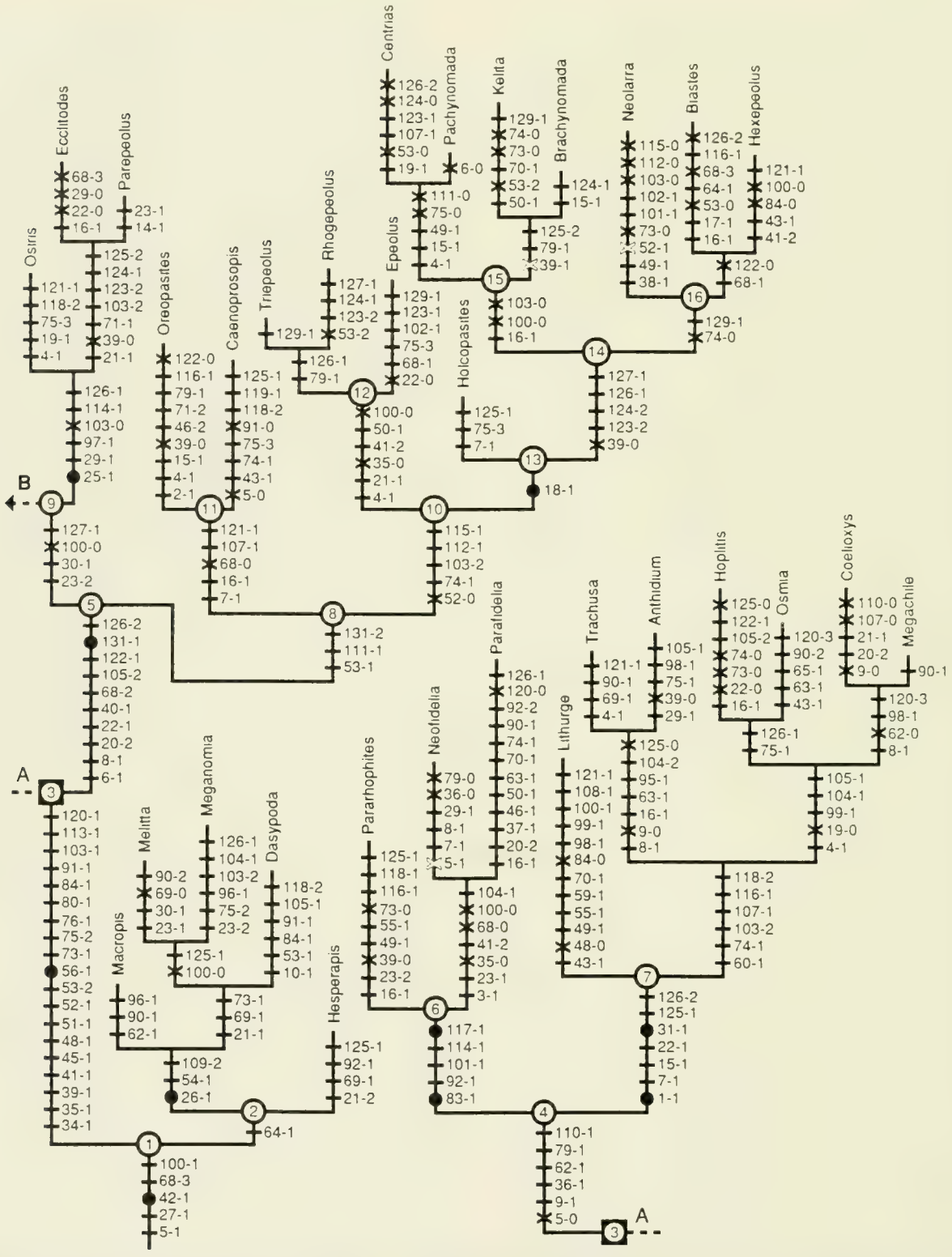
Node 29 is supported by Characters 3-2 (facial foveae) and 49-1 (incised base of labial palpus), which reverse to 3-1 and 49-0 in Node 33 and thus characterize the Exomalopsini. Moreover Character 75-1 is a reversal from 75-2, and goes back to 75-2 in Node 33. For further consideration of the Exomalopsini, see Silveira (1993).

Node 32 is supported by Character 19-1 which, however, appears in many other parasitic groups, but not in pollen-collecting bees. It is probably a convergent feature of parasitism rather than an indication of phyletic relationship. The other characters on this node are weak; the node itself should probably be eliminated in favor of a polytomy at Node 19.

Node 34 (Emphorini) is supported by Character 67-1, which is unique to the Emphorini. Character 11-1 (internal antennal sclerite) appears elsewhere in *Coelioxoides* and is only partly developed in *Ancyloscelis*.

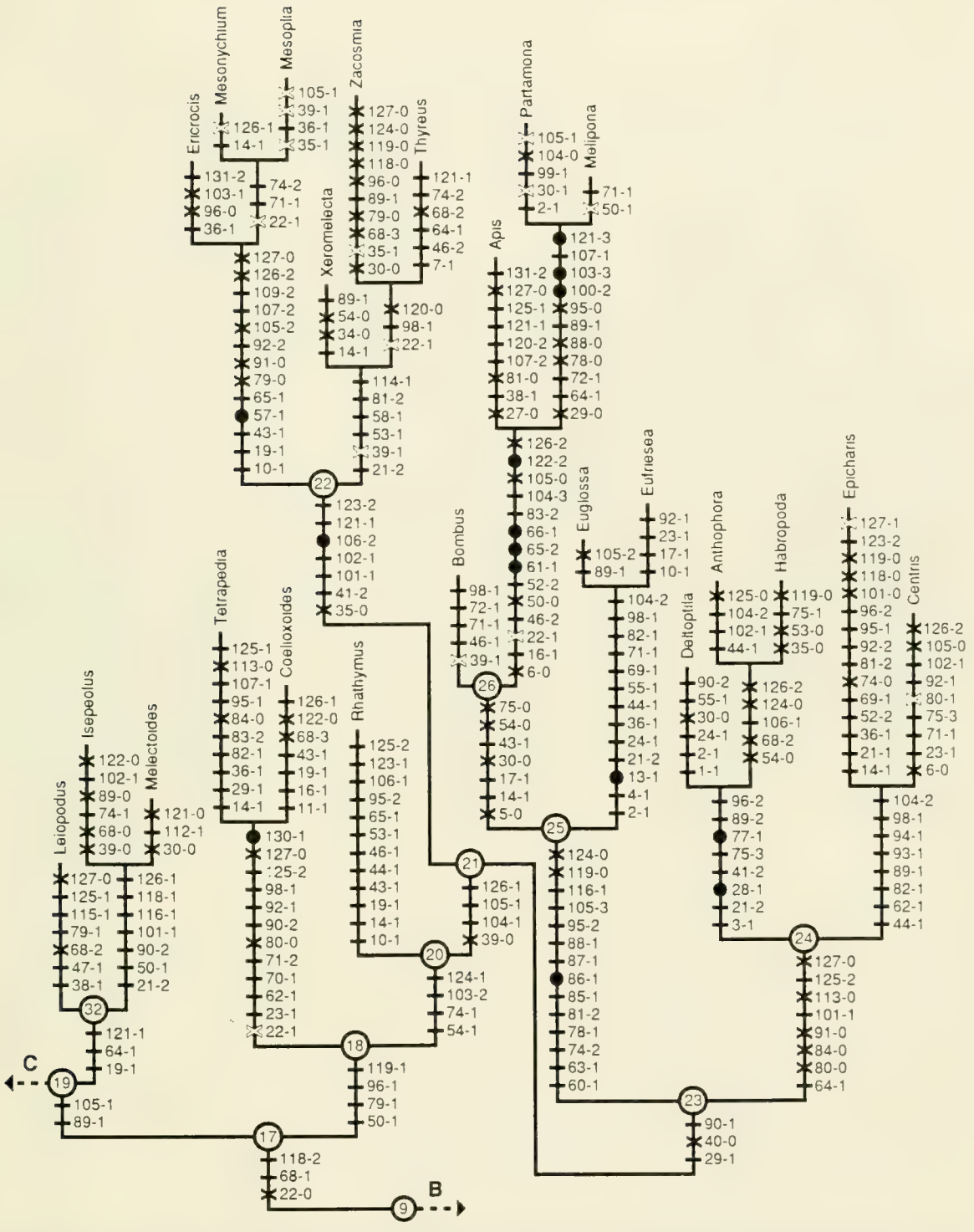
Node 38 (Eucerini + *Tarsalia*) is supported by Character 124-2, which appears also in Allodapini and Nomadinae but is so different as to be a good eucerine + ancyline character.

Node 39 (Eucerini) is supported by Character 12-1, which is unique for this group.



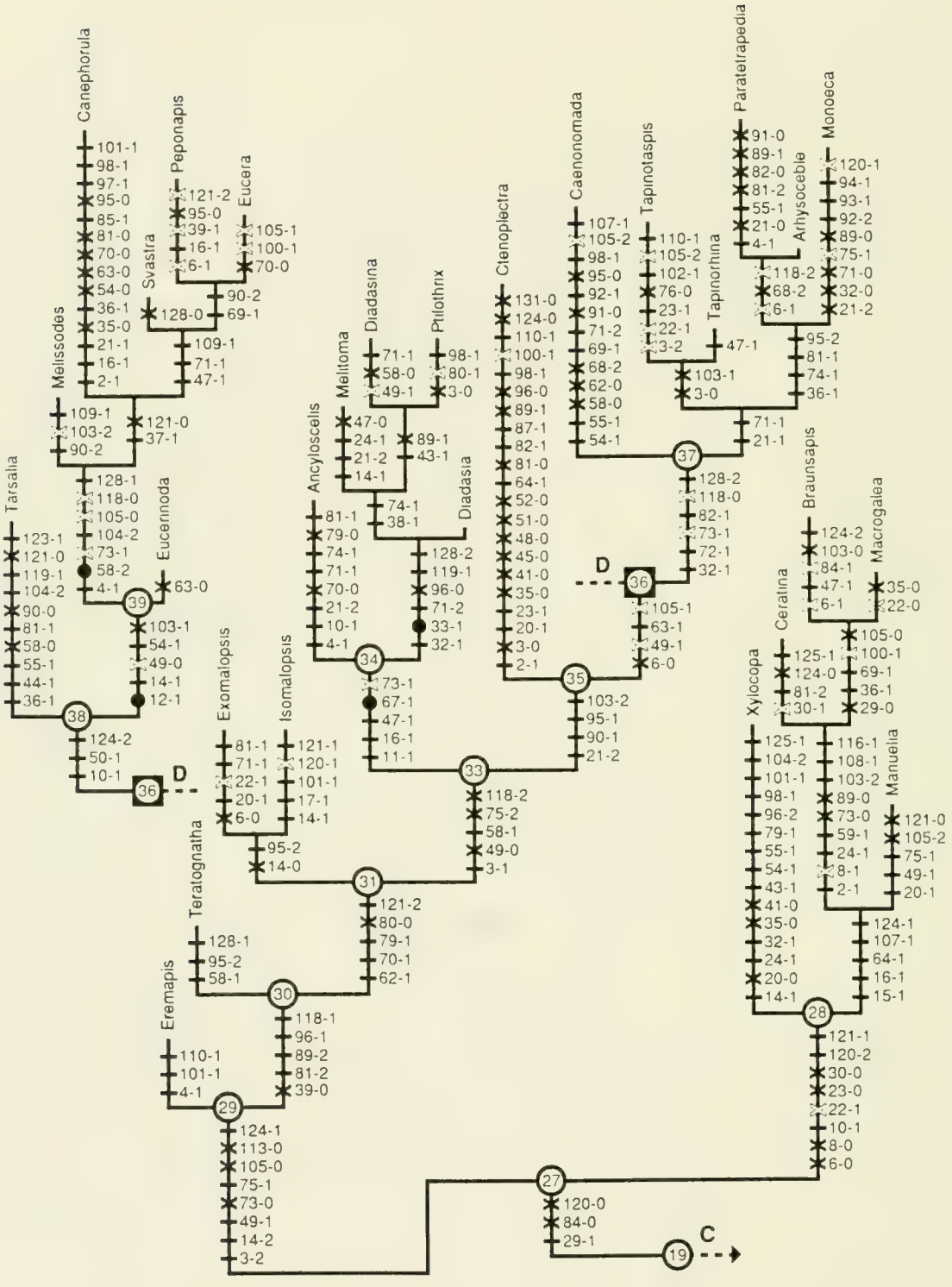
Cladogram 1a. One minimum-length tree based on Analysis A showing relationships based on adult characters among representative genera of long-tongued bees. The base of the cladogram is at the lower left of the first page. Characters are numbered according to the Annotated List of Adult Characters. Character transformation is symbolized as follows: dots indicate changes that occur

→



once in the tree, bars indicate changes that also occur in parallel elsewhere in the tree, black crosses indicate reversals to a state already present basally in the tree, white crosses indicate re-reversals. Only nodes referred to in the text are numbered. Capital letters and arrows indicate continuation of the tree on another page. Capital letters and black squares serve to match branches of the tree in the same page. Node 2 subtends the Melittidae; 4, the Megachilidae; 8, the Nomadinae; 25, the apine clade; and 28, the Xylocopinae.

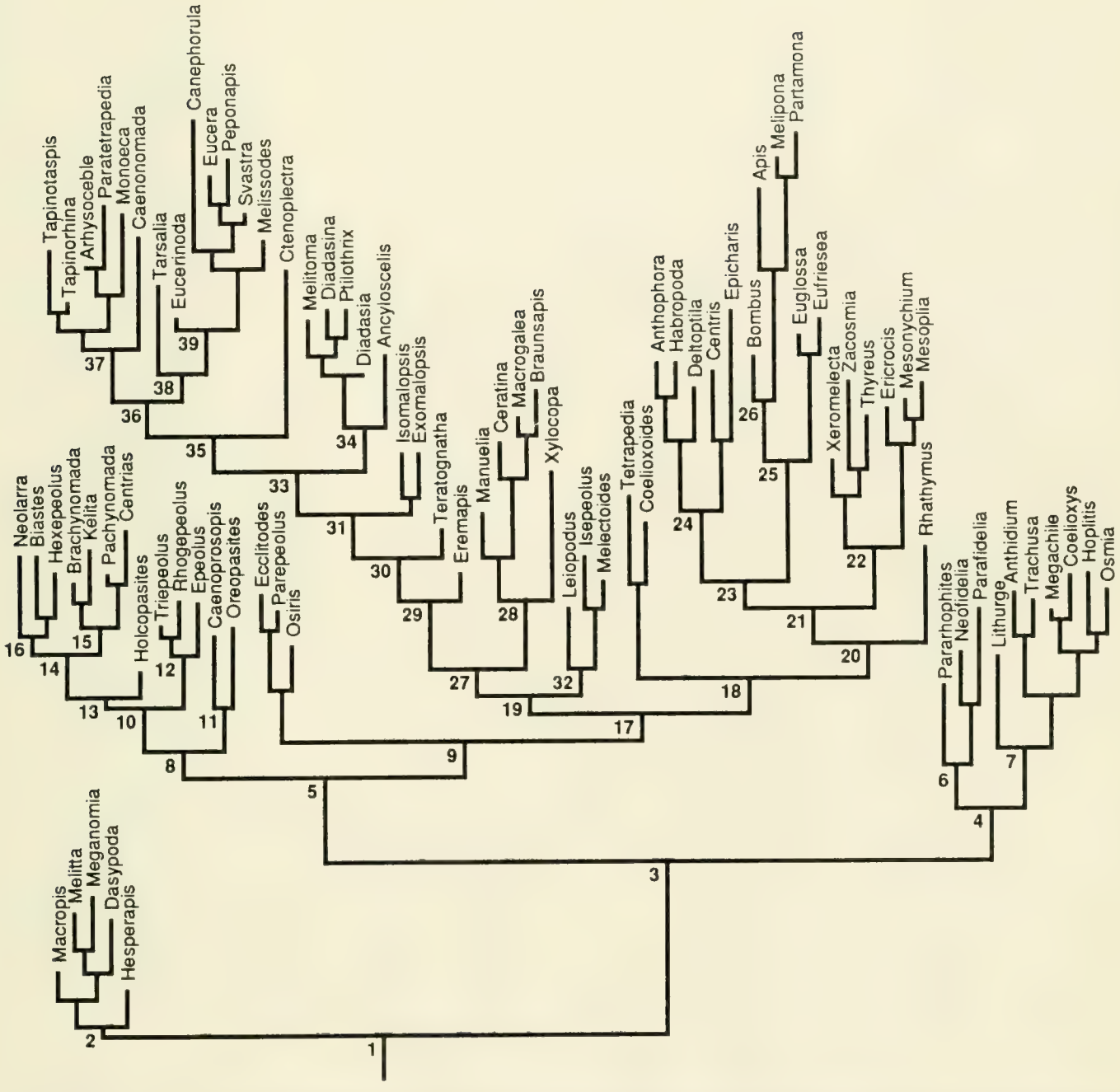
Continued on page 148



Cladogram 1a, continued.

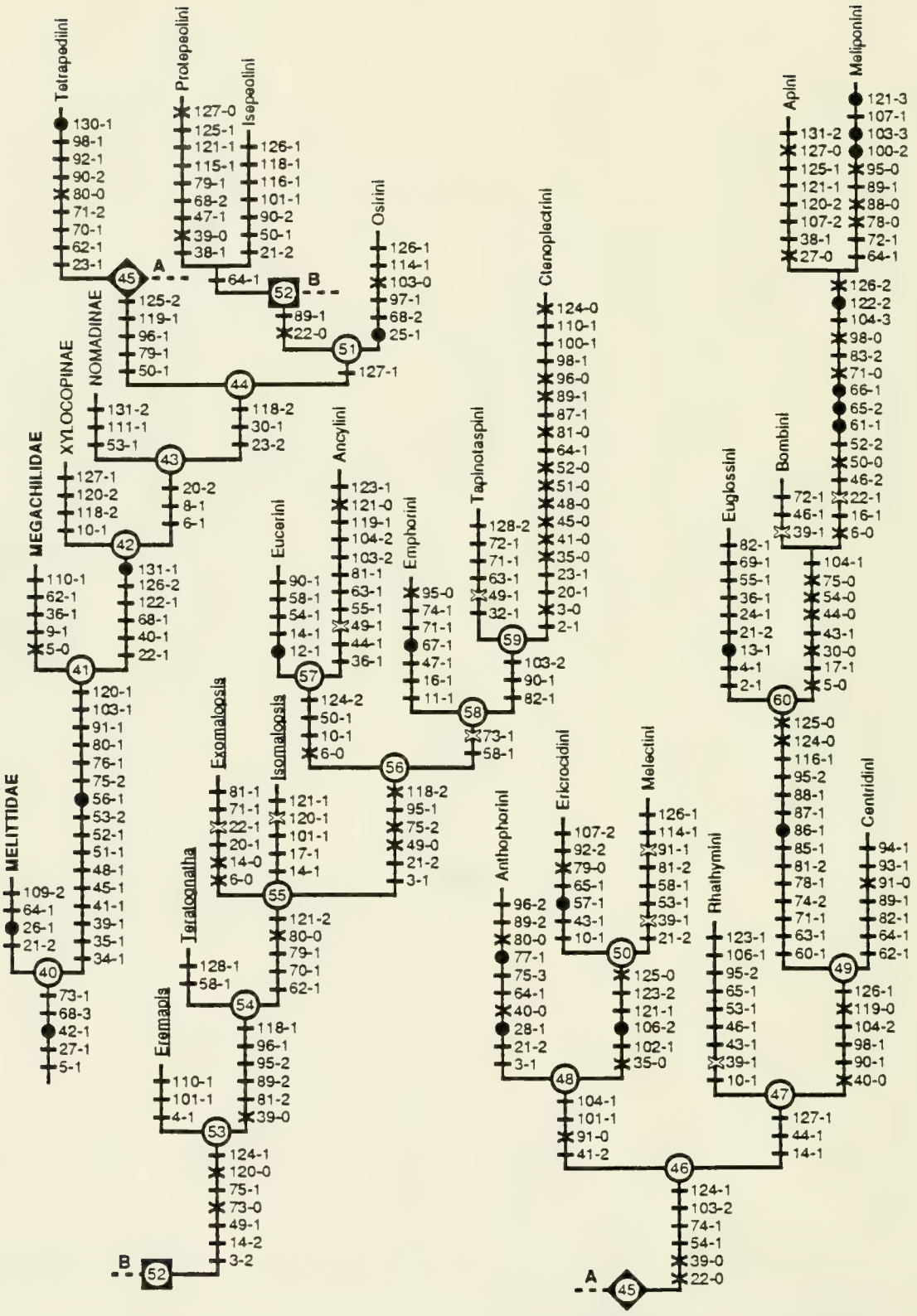
Analysis B: As explained above, this analysis contributed nothing of importance to our understanding of phylogeny since the trees produced were very similar to those of Analysis A. On the other hand, Analysis B added to our confidence since we could examine all the shortest trees. The fact that they were similar to the subset examined in Analysis A provides important support for this analysis.

In Analysis B the number of submarginal cells (Character 100) does not reverse from two to three, as in Analysis A.



Cladogram 1b. Summary of Cladogram 1a with characters omitted. Lengths of vertical lines are proportional to the numbers of characters.

Analysis C: (Note that node numbers 1-39 are for Analysis A, Cladograms 1a, 1b, while numbers 40-60 are for Analysis C, Cladogram 2a, 2b.) Cladogram 2a, based on Analysis C (five characters associated with parasitism omitted), gives some striking rearrangements relative to Analysis A. There are no longer characters of parasites in the stem from which nonparasitic taxa seem to be derived. The Xylocopinae become the first branch of the Apidae, between Megachilidae and Nomadinae. In connection with this, Node 42 is supported by Characters 40-1, 68-1, 122-1, and 131-1. Character 126-2 (loss of volsella) is reversed higher in the cladogram, which is not evolutionarily likely. The support of the Xylocopinae lacks four reversals shown in Node 28 of Cladogram 1a; these characters appear in Nodes 43



Cladogram 2a. Basal parts (to families, subfamilies, and tribes) of tree based on adult characters, Analysis C (five characters related to parasitism omitted). The base of the cladogram is at the left.

Cladogram 2b. Summary of Cladogram 2a, as consensus tree. Lengths of vertical lines are proportional to the number of characters.

and 44. These nodes are supported by characters that were reasonably strong in Analysis A.

Node 45 is essentially like Node 18. Also the Tetrapediini is supported by largely the same characters in Analyses A and B but Nodes 46 and above are substantially rearranged. The Anthophorini and Centridini are dissociated, the latter becoming the sister group of the apine group of tribes. The consensus tree (Cladogram 2b) shows a polytomy of four branches: (a) Centridini + the apine clades, (b) Anthophorini, (c) Rhathymini, and (d) Melectini + Ericrocidini.

Node 51 is supported only by Character 127-1 (spatha). As noted in Analysis A, this feature appears in branches throughout the Apidae and should probably be in Node 42, with losses in certain taxa. Thus 127-1 is probably plesiomorphic for Apidae; if so, Node 51 would collapse.

Node 52 is supported by Character 89-1 which, however, appears also in Centridini and as 89-2 in Anthophorini.

The Protepeolini (*Leiopodus* in Cladogram 1a, 1b) and Isepeolini are united only by Character 64-1 (prosternal arms). A polytomy at 52 is a likely conservative interpretation.

The positions of *Eremapis* and *Teratognatha* are supported by Nodes 53 and 54, which have almost the same sets of characters as 29 and 30, Cladogram 1a. Node 55 is identical to 31. *Isomalopsis* and *Exomalopsis* are united in some of the Analysis C trees as is shown in Cladogram 1a. See Silveira (1993) for reanalysis of the Exomalopsini.

The remainder of Cladogram 2a is rather different from Cladogram 1a and the topology of different versions is diverse. The consensus tree shows a five-part polytomy as follows: (a) Ancylini (*Tarsalia* in Cladograms 1a and 1b), (b) Ctenoplectrini, (c) Tapinotaspini, (d) Emphorini, and (e) Eucerini. As in Cladograms 1a and 1b, *Canephorula* is in the midst of Eucerini, not a basal branch. Of the three topologies for this part of the cladogram found in Analysis C, one is shown in Cladogram 2a and 2b; another is as in Cladograms 1a and 1b. A third shows the following arrangement: ((((Ctenoplectrini, Tapinotaspini) Eucerini) Emphorini) Ancylini).

Analysis D: For this analysis (parasitic taxa excluded), a summary based on the consensus tree is presented as Cladogram 3a. Compared to Cladograms 1 and 2, various similarities are apparent. The Megachilidae are monophyletic and almost identical. The Xylocopinae are positioned as in Cladograms 2a and 2b and identical in branching pattern. (See the reanalysis of the Xylocopinae in the discussion of Classificatory Results.) As in Analyses A, B and C, the Exomalopsini constitute a paraphyletic group with the taxa arranged in the same way. (See the reanalysis by Silveira, 1993.) This group is located, however, between the Xylocopinae and all other Apinae, which are based on a large polytomy. In Analyses A, B and C there are two major branches separated at nodes 17 and 44 (see Cladograms 1 and 2). Such branches are not evident in Cladogram 3a, or in the individual trees upon which the consensus tree was based. The eight branches of the large polytomy in the consensus tree are as follows: (a) *Tetrapedia,* (b) *Tarsalia,* (c) *Eucerinoda,* (d) *Ctenoplectra,* (e) Tapinotaspini, (f) Emphorini, (g) Eucerina, and (h) a branch including Anthophorini, Centridini, and the apine clade. Thus a feature of Cladogram 3a is the association of the taxa listed under (h), as in Cladograms 1a and 1b.

With successive approximations character weighting by F. Silveira, all eight trees were alike in topology except for differences within the Melittidae and in the relative positions of *Isomalopsis, Exomalopsis,* and the stem leading to most other Apinae. The consensus tree is therefore completely resolved for L-T bees except for one polytomy. The topology for the Megachilidae, Xylocopinae, *Eremapis, Teratognatha,* and the polytomy (*Exomalopsis, Isomalopsis,* other Apinae) is as in Cladogram 3a. The other Apinae are divided into two main branches, as in Cladograms 1a, 1b, 2a, and 2b; unlike those cladograms, however, the Eucerini are in the same major branch as the apine clade and the Anthophorini, although near the base of this group and thus near the other branch. The topology for the Apinae above the polytomy is shown as light lines, Cladogram 3b.

Analysis E: Based on larvae, this analysis results in two islands of trees; the major one (176 trees) is summarized by a consensus tree, Cladogram 4. The minor island's consensus tree (based on 16 trees) is discussed below. In bees, larvae that spin cocoons are usually different in labial and other characters from larvae that have lost cocoon-spinning behavior. However, within L-T bees these differences do not appear to influence the tree greatly, for most L-T bees spin cocoons. Characters 43-2, 47-0, 49-1, 50-2, and 51-1 tend to appear among non-cocoon-spinning taxa; such taxa among L-T bees are *Thyreus, Epicharis,* Anthophorini, Xylocopinae, and Nomadinae, as well as one group of Melittidae.

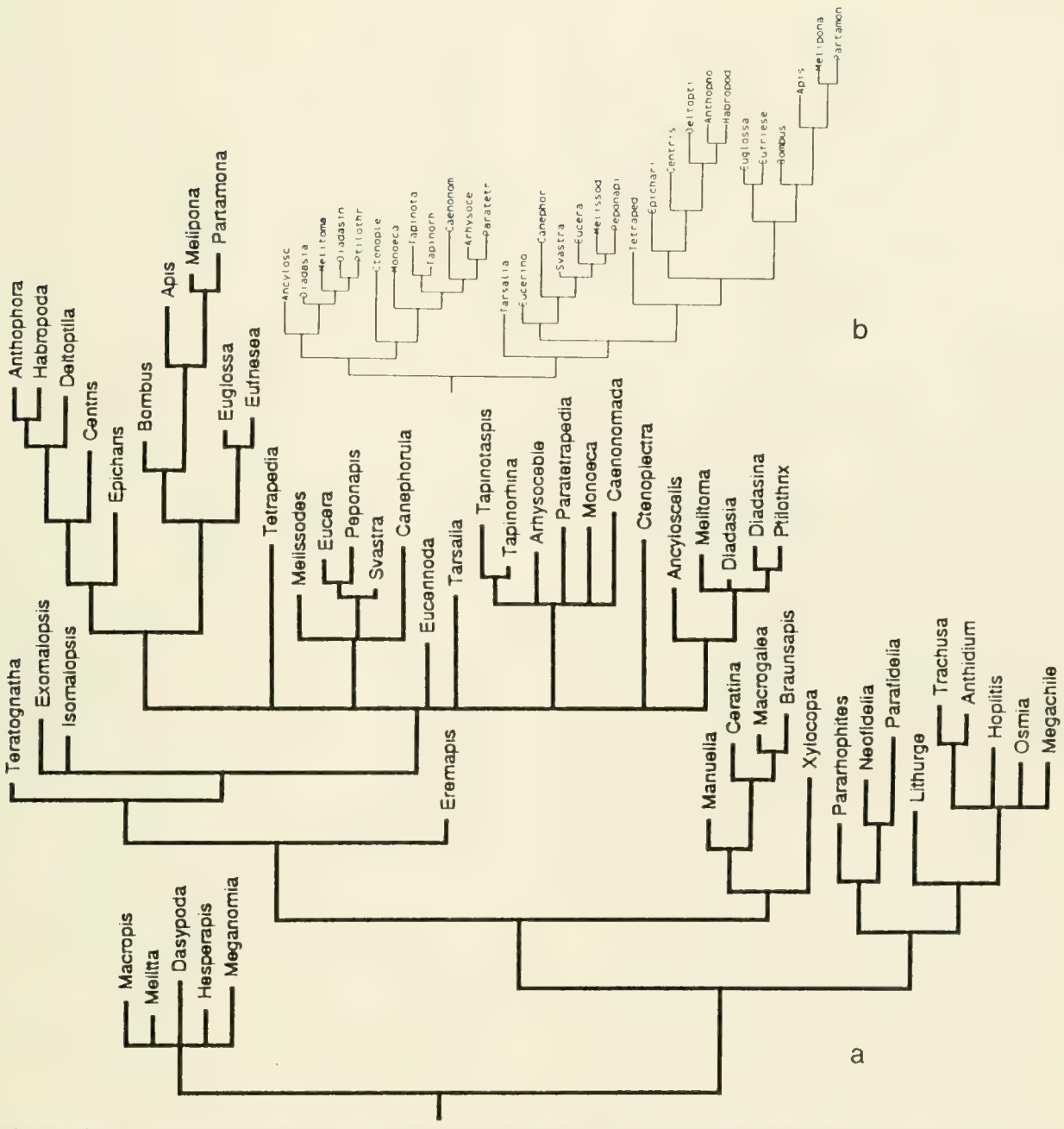
In the consensus tree for the major island of trees, the Nomadinae with *Isepeolus* form a clade. The Brachynomadini is the basal nomadine group in the consensus tree, in the trees of the minor island, and in Rozen, Eickwort and Eickwort's (1978) cladogram based on larvae. Also Neolarrini and Biastini are sister groups in these three analyses as are *Epeolus* and *Triepeolus.* Otherwise the three cladograms are quite dissimilar. We do not wish to support the paraphyly of Ammobatini indicated in Cladogram 4 as well as in the analysis of the minor island of trees.

The rest of the taxa in the consensus tree for the major island arise from a large polytomy (6 branches) as shown in Cladogram 4. One member of this polytomy contains *Rhathymus,* the Ericrocidini, Melectini, Ctenoplectrini, Megachilidae and the tribes of the apine clade. Within this large group, the most surprising subgroup consists of the apine complex and most Megachilidae, with the Megachilidae as a whole being a paraphyletic unit from which the apine complex arose. Since we did not directly examine the larvae, but merely used a table of characters, we only present this strange result, which disappears when larval and adult characters are used together (Analysis H, Cladogram 5).

The minor island of trees gives strange results that we find not useful. The Nomadinae are the sister group of *Dasypoda* in the Melittidae. In the consensus tree there is a trichotomy consisting of *Capicola, Hesperapis,* and *Dasypoda* + Nomadinae. This trichotomy is the sister group of all the other bees in our study, which are divided into two groups. One consists of *Exomalopsis, Paratetrapedia,* the Eucerina, Emphorina (the last two as sisters), the Anthophorini, Centridini, *Leiopodus,* the last as the sister to Xylocopinae. The other consists of the rest of the Melittidae, *Isepeolus,* the Melectini, Ericrocidini, *Ctenoplectra,* and the Megachilidae plus the tribes of the apine clade, the last arranged as in Cladogram 4.

Analyses F and G: These analyses were designed to compare phylogenies based on larvae (F) and on adults (G). Many of the groups were alike in the two analyses, but the connections (i.e., the relationships of major groups) were often quite different. Comparing the consensus trees, the following taxa or groups appear in both:

1. Megachilidae. For adults the arrangement is similar to that of Analysis A. For larvae, Megachilidae are the sister group to the apine clade and most genera form a polytomy except that *Neofidelia* and *Parafidelia* form a sister group arising from the polytomy.



Cladogram 3: a. Consensus tree based on adult characters, Analysis D (all cleptoparasitic taxa omitted). Lengths of vertical lines are proportional to numbers of characters. **b.** The same, large polytomy of 3a, resolved by use of successive approximations character weighting. (This is a consensus tree; polytomies occurred elsewhere.) The generic names are written out in full in Cladogram 3a.

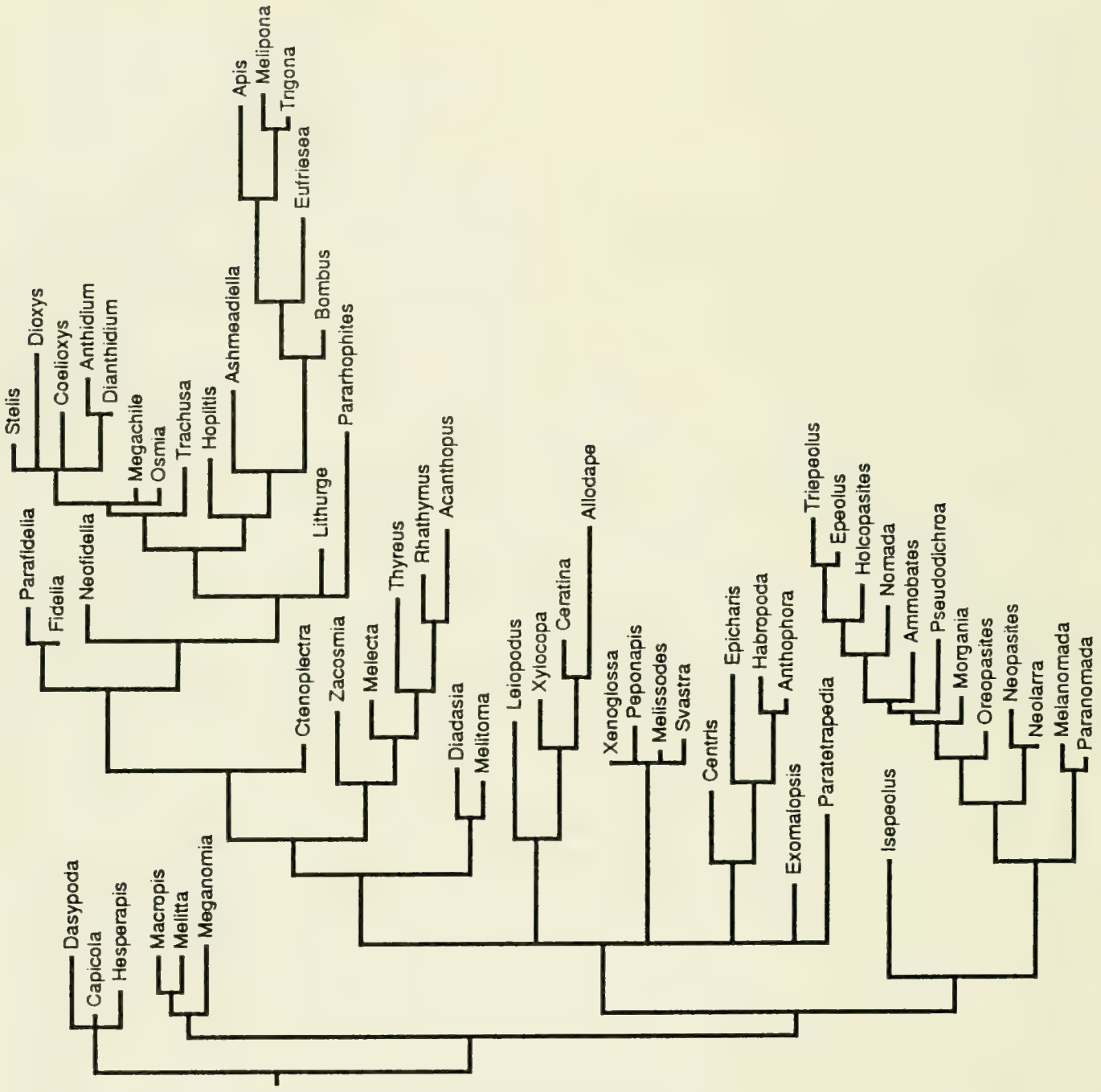
2. Nomadinae.

3. Xylocopinae. For adults the Xylocopinae is part of the large polytomy including all L-T bees except Megachilidae and Nomadinae. For larvae the Xylocopinae plus *Leiopodus* constitute the sister group to *Exomalopsis* + Emphorini + Eucerini.

4. Anthophorini—Centridini. For adults these tribes, as sisters, arise from the large polytomy. For larvae these tribes constitute the sister group to Xylocopinae + *Leiopodus* + *Exomalopsis* + Emphorini + Eucerini, and the Anthophorini arise from a paraphyletic Centridini.

5. The apine clade. For adults this clade arises from the large polytomy, *Bombus, Eufriesea,* and the rest forming a trichotomy. For larvae, this clade is the sister group of Megachilidae; *Bombus* is the first branch, *Eufriesea* the next.

6. Emphorini. For adults, part of a polytomy including *Exomalopsis, Paratetrapedia,* and Eucerini. For larvae, the sister group to Eucerini.



Cladogram 4. Consensus tree based on the larger island of minimum-length trees using larval characters, Analysis E. Lengths of vertical lines are proportional to numbers of characters.

7. Eucerini. See comments on Emphorini.

For adults, the Apidae are the sister group to Megachilidae, the two families together constituting the L-T bees. For larvae, the megachilids are a subgroup within the other L-T bees and sister group to the apine clade. But at the subfamily and tribal levels most genera fall within the same taxa (1-7 above) whether larvae or adult characters are used. The exceptions are eight genera. Two that clearly constitute the Melectini (*Zacosmia* and *Thyreus*) in the adult cladogram are not widely separated in that for larvae. The other six seem to occupy quite unrelated positions when one compares the trees based on larvae and on adults. They are *Ctenoplectra*, *Exomalopsis*, *Isepeolus*, *Leiopodus*, *Paratetrapedia* and *Rhathymus*. Each of these lacks close relatives available as both larvae

and adults for our study; they are thus not closely related to other taxa in Analysis H.

From the above comments it is apparent that while the smaller groups (largely subfamilies and tribes, but including Megachilidae) usually are found in both the larval and adult cladograms, the arrangement of these groups is in some cases very different. Thus while larval characters usually support adult-based smaller groups, they do not always support the larger groups based on adult characters.

Analysis H: This analysis was based on larvae and adults combined, using the united matrices for Analyses F and G; it resulted in the single minimum-length tree shown in Cladogram 5. In a few features it is similar to the cladogram based on larval characters (Cladogram 4), but in other respects it resembles those based on adults. The following are interesting features of Cladogram 5.

1. Melittidae. As in the larval analysis (Cladogram 4), the melittids are divided and paraphyletic.

2. Megachilidae. This family is not associated with Apini and its relatives, as in the larval analysis, but within the family the Fideliinae is paraphyletic, in contrast to Analyses A-D and G, Cladograms 1-3. Moreover, *Hoplitis* and *Osmia* are separated rather than being sister groups as in Analysis A (Cladograms 1a and 1b).

3. Nomadinae. The included tribes are not arranged as in the other analyses. See the reanalysis under Classificatory Results.

4. *Isepeolus* and *Leiopodus* are separated, but as in Cladograms 1a, 1b, 2a, and 2b, appear near the base of the Apinae.

5. There are not two major branches such as separate at Nodes 17 and 44, Cladograms 1a, 1b, 2a, and 2b. The tribes of the apine complex are arranged as in Cladograms 1a and 1b but are not closely associated with Anthophorini or Centridini.

6. As in Cladograms 3a and 3b, *Centris* and *Epicharis* form a paraphyletic group from which the Anthophorini arose, instead of being a sister group to Anthophorini as in Cladograms 1a, 1b, 2a, and 2b.

7. *Exomalopsis* and *Paratetrapedia* are sister groups, together the sister group to Emphorini + Eucerini, this whole complex being the sister group to *Ctenoplectra*.

Many of the deviations from Analyses A to C are a result of the limited number of taxa for which larval data are available. For example, *Exomalopsis* cannot appear near other genera of Exomalopsini because there are no larval data for the latter.

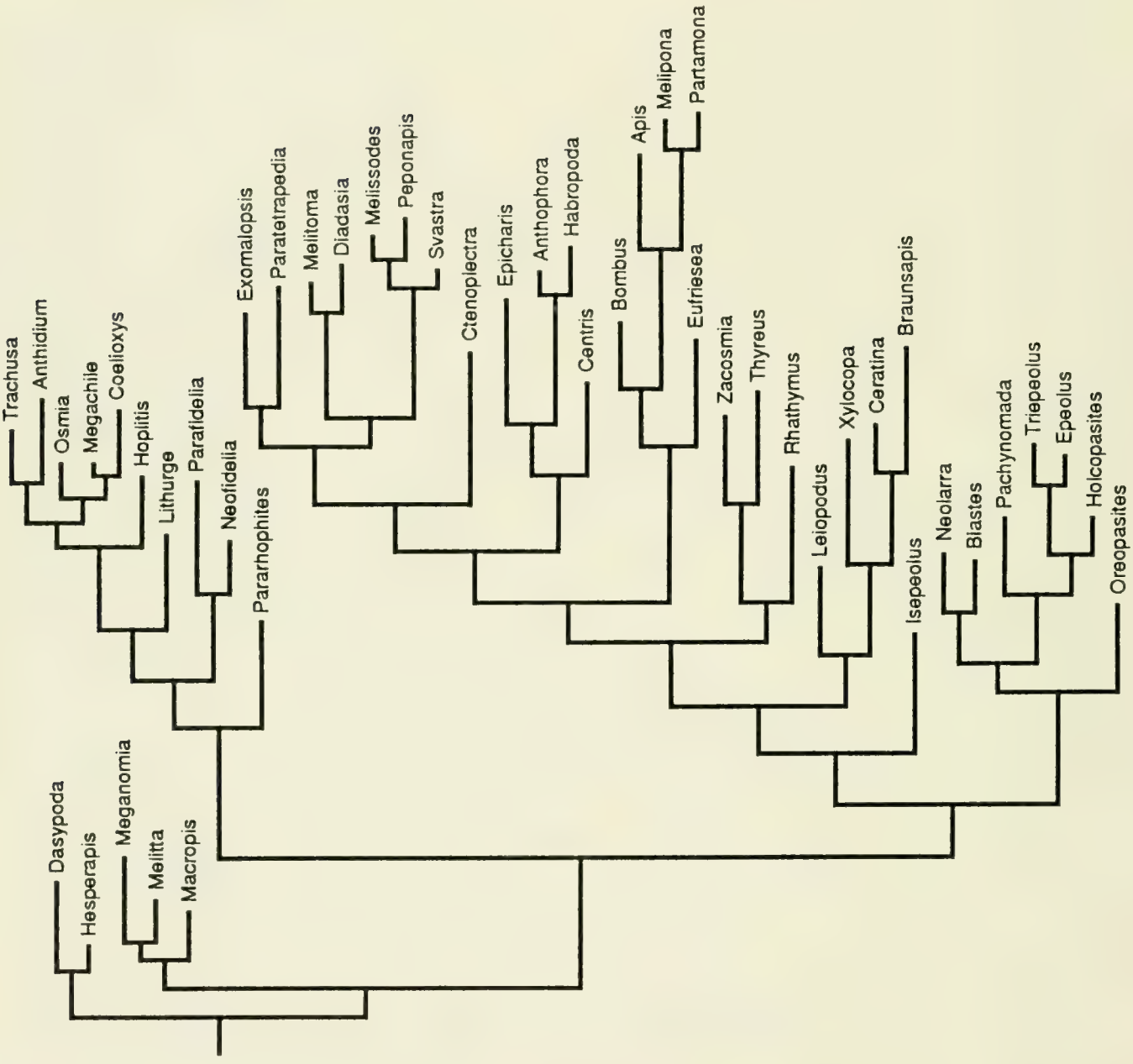
CLASSIFICATORY RESULTS

At least the classificatory levels, and often other features of classifications, are subjectively determined. No one of our trees can be used alone for developing a classification. Analysis A has the full complement of adult characters and available taxa but results in cladograms in which features of parasitic bees evolve into those of nonparasitic bees, among other problems. Analysis C partly corrected this problem and is probably our best tree on which to base a classification, although it suffers from collapsing of certain nodes as explained for Analysis B in the preceding section. Analysis D, performed to further clarify the problems arising from parasitic bees, lacks all parasitic taxa. All other analyses lack many taxa because of the sparse information on larvae.

The following classification, therefore, is based on available information from the various analyses. Except for the Exomalopsini, all family-group taxa are found to be monophyletic in several or all of our analyses. The only commonly accepted family-group taxon of L-T bees not included in our study for lack of specimens to dismember, the Townsendiellini, is included on the basis of another study (Roig-Alsina, 1991). The genera included in the study, and occasionally others for clarification (the latter in parentheses) are listed.

Megachilidae
- Fideliinae
  - Pararhophitini—*Pararhophites*
  - Fideliini—*(Fidelia), Neofidelia, Parafidelia*
- Megachilinae
  - Lithurgini—*Lithurge*
  - Anthidiini—*Anthidium, (Dioxys), Trachusa*
  - Megachilini—*Coelioxys, Megachile*
  - Osmiini—*Hoplitis, Osmia*

Apidae
- Xylocopinae
  - Xylocopini—*Xylocopa*
  - Manueliini—*Manuelia*
  - Ceratinini—*Ceratina*
  - Allodapini—*(Allodape), Braunsapis, Macrogalea*
- Nomadinae
  - Ammobatini—*Ammobates, Oreopasites,*
  - Caenoprosopidini—*Caenoprosopis*
  - Neolarrini—*Neolarra*
  - Townsendiellini—*(Townsendiella)*
  - Nomadini—*Nomada*, subgenera *Centrias* and *Pachynomada*
  - Biastini—*Biastes, (Neopasites)*
  - Hexepeolini—*Hexepeolus*
  - Ammobatoidini—*(Ammobatoides), Holcopasites*
  - Brachynomadini—*Brachynomada, Kelita, Melanomada*
  - Epeolini—*Epeolus, Rhogepeolus, Triepeolus*
- Apinae
  - Tetrapediini—*Coelioxoides, Tetrapedia*
  - Rhathymini—*Rhathymus*
  - Euglossini—*Eufriesea, Euglossa*
  - Bombini—*Bombus*
  - Apini—*Apis*
  - Meliponini—*Melipona, Partamona, (Trigona)*
  - Centridini—*Centris, Epicharis*
  - Anthophorini—*Anthophora, Deltoptila, Habropoda*
  - Ericrocidini—*Eriocrocis, Mesonychium, Mesoplia*
  - Melectini—*(Melecta), Thyreus, Xeromelecta, Zacosmia*



Cladogram 5. Minimum-length tree based on larval and adult characters, Analysis H. Lengths of vertical lines are proportional to numbers of characters.

Osirini—*Ecclitodes, (Epeoloides), Osiris, Parepeolus*
Protepeolini—*Leiopodus*
Isepeolini—*Isepeolus, Melectoides*
Exomalopsini—*Eremapis, Exomalopsis, Isomalopsis, Teratognatha*
Ancylini—*(Ancyla), Tarsalia*
Eucerini
  Eucerinodina—*Eucerinoda*
  Eucerina—*Canephorula, Eucera, Melissodes, Peponapis*
Emphorini
  Ancyloscelina—*Ancyloscelis*
  Emphorina—*Diadasia, Diadasina, Melitoma, Ptilothrix*
Ctenoplectrini—*Ctenoplectra*

Tapinotaspini—*Caenonomada, Monoeca, Paratetrapedia* and subgenus *Arhysoceble, Tapinotaspis* and subgenus *Tapinorhina*

Our cladograms should not be used to develop a classification of Melittidae. We included melittid genera for our analyses as an outgroup. To develop a classification of that family, more genera, probably other characters, and outgroups among the S-T bees should be used. Larvae suggest that the family Melittidae is not monophyletic and Michener (1981) found no synapomorphies for the family. We, however, found the small intercalary sclerite between the cardo and stipes (Character 26-1) which appears to be a family level synapomorphy. The sclerite, however, is sometimes exceedingly small and inconspicuous.

The Fideliinae, with its subdivision into tribes Pararhophitini and Fideliini, appears in all trees based on Analyses A to D. This arrangement, although not previously formalized, is similar to that which Rozen (in McGinley and Rozen, 1987) envisioned. The Fideliinae is strongly supported by Characters 83-1, 92-1, 114-1 and 117-1, the first and last of which are unique to this subfamily. Another unique character of the subfamily is the cocoon mixed with sand previously ingested by the larva (McGinley and Rozen, 1987).

The position of *Lithurge* as the sister group of the rest of the Megachilinae appears in all trees based on Analyses A, D and H. Synapomorphies of the tribe Lithurgini are listed by Michener (1983). If one wishes to use the category subtribe, then the Lithurgini and Megachilini could be the two tribes of Megachilinae, the Megachilini being divided into the subtribes Anthidiina, Megachilina, and Osmiina, although in the consensus tree of Analysis A *Osmia* and *Hoplitis* arise separately from the same polytomy as the other two tribes. We prefer the classification shown above because there is no objective basis for changing the established recognition of Anthidiini, Megachilini and Osmiini as tribes.

The subfamily Xylocopinae appears as a recognizable group in all trees. Its position at the base of the Apidae is shown in Analyses C and D (Cladograms 2 and 3) and it is near the base (above Nomadinae) in Analysis H (Cladogram 5). The sister group relationship of Xylocopinae to the apine clade indicated by Sakagami and Michener (1987) is seemingly incorrect. As indicated at that time, it was based largely on the similar structure of S8 of the male, which is now recognized as a plesiomorphy. There are, however, behavioral characters such as food storage outside the larval cells that support the supposed relationship of Xylocopinae with the apine clade. We now believe these behavioral similarities to be convergent.

Within the Xylocopinae, our analyses show *Xylocopa* to be the first branch, while Sakagami and Michener (1987) found *Manuelia* to be in that position, i.e., their tree differed from ours in that *Manuelia* and *Xylocopa* exchanged positions. We therefore reanalyzed the Xylocopinae, using the 41 characters of the present study that vary among our exemplars of the subfamily, repolarized as necessary according to the condition found in Node 42, and seven additional characters used by Sakagami and Michener (1987, characters 6, 16, 21-23, 26, 27). The outgroup used was all plesiomorphies (all 0's). The result was two equally parsimonious trees (statistics: L 64, T 2, ci 82, ri 71). The difference between the two trees is in the positions of *Xylocopa* and *Manuelia,* one having the topology of Sakagami and Michener (1987), the other that of the present study. If one must choose, CDM favors *Manuelia* as sister group to the others because of the strong synapomorphy of S8 of the male for the other tribes, countered by a plesiomorphic S8 in *Manuelia* (Sakagami and Michener, 1987). (It should be noted that Figure 10 of Sakagami and Michener [1987] is inverted; the truncated spiculum is directed upward on the page.)

The relationships within the subfamily Nomadinae as shown in Analysis A (Cladograms 1, 1a) differ in several respects from those based on larvae and those given by Roig-Alsina (1991). A reanalysis was made of Nomadinae alone, using 36 adult characters from the present study repolarized as necessary according to the condition found in Node 43, and adding nine other characters used by Roig-Alsina (1991, characters 4-8, 10-13) but omitted from our study of L-T bees. *Biastes* was coded as plesiomorphic for Roig-Alsina's character 12 (degree of fusion of furcula) because of the plesiomorphy seen in its near relative, *Rhopalolemma.* A single shortest tree (L 114, T 1, ci 46, ri 56) was found. It is like that of Roig-Alsina (1991) in topology except that the positions of *Hexepeolus* and *Nomada* are reversed. This reanalyzed tree of Nomadinae is presumably more reliable than that shown in our cladograms.

Our trees and Roig-Alsina's based on adults show *Oreopasites* and *Caenoprosopis* as the sister group to the rest. We considered using this division to recognize two tribes, each with subtribes. The larvae do not at all support such tribes (see Analysis F and Rozen, Eickwort and Eickwort, 1978) and in the study by Roig-Alsina (1991) *Townsendiella* could be equally parsimoniously placed in either tribe. Furthermore, the detailed analysis by Alexander (1990) does not demonstrate the two major groups within the Nomadinae that we found. We therefore retain the numerous tribes of previous works, and for consistency add two new ones, the Hexepeolini (new family-group name for *Hexepeolus*) and the Brachynomadini (new family-group name for *Brachynomada, Kelita, Melanomada, Paranomada,* and *Triopasites*). The Brachynomadini is the melanomadine complex of Alexander (1990).

The reason for the great difference between our results and Alexander's may include the following: He included taxa that we do not believe are Nomadinae; if we are correct his group was not monophyletic. Moveover, on the basis of information then available, he considered the Exomalopsini to be the outgroup; his polarization of some characters would therefore have differed from ours.

The Tetrapediini includes both *Tetrapedia* and the parasitic genus *Coelioxoides* in Analyses A and C (Cladograms 1a, 1b). Thus the placement of *Coelioxoides* by Roig-Alsina (1990) is supported. The two genera are so different (*Coelioxoides* being parasitic), however, that they might well be placed in

separate subtribes. Since each would include only one genus, such subtribes would serve little purpose.

In Analyses A and G the Anthophorini and Centridini are sister groups whereas in Analysis C they are widely separated, and in D to F and H Centridini appear as paraphyletic with Anthophorini as the sister group either to *Epicharis* (Analyses E, F, H) or to *Centris* (Analysis D). We prefer to regard the Anthophorini and Centridini as separate, probably monophyletic tribes (see, however, the cladograms of Silveira, 1993). The association of the three genera of Anthophorini in our study is consistent and we do not believe that the tribal name Habropodini used by Brooks (1988) is necessary.

The tribes of the apine clade are Euglossini, Bombini, Apini and Meliponini. One of us (AR-A) would prefer to regard these as subtribes of a tribe Apini, to show their relationship to one another. The other (CDM) argues that the great differences among the four taxa justify recognition of each at the tribal level.

The many common characters of the apine clade (Nodes 25, 60) have been used in the past to justify family status. Michener (1944), however, united the Apidae and Anthophoridae under the former name; we support this conclusion, although Michener (1965) later recognized the families as separate. Those who would recognize a paraphyletic Anthophoridae from which Apidae arose must demonstrate a major gap in morphology between the two. In view of the strength of Nodes 25 and 60, this is surprisingly hard to do when both sexes, both female castes, and all included taxa are considered.

The arrangement of the four tribes of the apine clade is the same for Analyses A, C, D, and H (Cladograms 1, 2, 3, and 5). This is one of Michener's (1990c) two preferred arrangements; the other was a dichotomous arrangement (Michener's Figure 1) which is not supported by our study. Our arrangement is also the same as that proposed by Prentice (1991).

There is no morphological support for the sister group relationship of Bombini and Meliponini proposed by Cameron (1991) on the basis of mitochondrial DNA sequences and by Sheppard and McPherson (1991) on the basis of ribosomal DNA sequences.

The Ericrocidini and Melectini appear as sister groups in Analyses A and C (Cladograms 1 and 2). Since the common characters that indicate their relationship (see discussion of Node 22 above) are not obviously convergent features related to parasitic habits, these two tribes may be derived from a common parasitic ancestor.

The position of Osirini, Protepeolini, and Isepeolini well separated from the Nomadinae support the recent and sometimes tentative removal of these groups from Nomadinae or placement of them as basal branches in analyses of parasitic, *Nomada*-like bees (see Alexander, 1990; Roig-Alsina, 1991; and Rozen, Eickwort and Eickwort, 1978).

The Protepeolini *(Leiopodus)* appear in different positions in different trees. The association with Isepeolini in Cladograms 1 and 2 is weak. The larval characters indicate wide separation of the two tribes (Cladogram 4) and this is maintained in Cladogram 5. The modification of the metasomal apex associated with egg laying by parasites is so different as to suggest separate origins for the two tribes from nonparasitic ancestors. In any event, it seems best to separate Protepeolini and Isepeolini at the tribal level since the evidence for a sister group relationship is weak.

Protepeolus Linsley and Michener is a junior synonym of *Leiopodus* Smith (Roig-Alsina, new synonymy) but the tribal name is still Protepeolini.

The Exomalopsini in all cladograms based on adults appears to be a paraphyletic unit. In Analyses A and C this tribe seems far from the base of the Apinae. However, when one considers the small number and weakness of characters of Nodes 9, 17, 19, and 27 or 43, 44, 51, and 52, the Exomalopsini are seen to fall rather near the base of the Apinae. In Analysis D (Cladogram 3) they form the base of the large sister group to the Xylocopinae and thus constitute the base of the Apinae, a position not inconsistent with the larval information (Analysis E, Cladogram 4); larvae have not been described except for *Exomalopsis*. In Analysis H (Cladogram 5), however, *Exomalopsis* appears with *Paratetrapedia* in the Tapinotaspini as the sister group to Emphorini and Eucerini.

As noted above in the discussion of Analysis A, Node 29 is supported by three characters that appear in that node, characterize the Exomalopsini, and reverse in Node 33. Further analysis will probably reveal more characters with this distribution and show that the Exomalopsini is monophyletic. We recognize it as a tribe even if it is paraphyletic. Reanalysis by Silveira (1993) has provided better but not decisive evidence that it is monophyletic.

Taxa sometimes included in the Exomalopsini that are here shown to be distinct and not necessarily closely related to it are the Ancylini, the Tapinotaspini, and the genus *Ancyloscelis* in the Emphorini.

The Ancylini (*Ancyla* and *Tarsalia*, only the latter included in our study) appears in Cladograms 1a and 1b as the sister group to the Eucerini; in the consensus tree for Analysis A, it is in a polytomy with *Eucerinoda* and the other Eucerini. In Analysis C the consensus tree shows it in a polytomy with four other taxa, one of which is the Eucerini. In Analysis D the consensus tree places *Tarsalia, Eucerinoda*, other Eucerini, and five other taxa in a polytomy. Our impression was that Ancylini represents a basal branch of the eucerine clade but since the evidence was not clear, we maintained Ancylini as a tribe. Silveira (1993), however, has reexamined the data, added *Ancyla* to his analysis, and concluded that a sister-group relationship to the Eucerini is not likely.

The Eucerini appear consistently as a clade including as its basal branch the Chilean genus *Eucerinoda*. Larvae of the latter are unknown but larval characters group other Eucerini (Cladogram 4). *Eucerinoda* lacks various features of the previously recognized Eucerini including the long paraglossae, hitherto considered a unique feature of the tribe. We therefore recognize two subtribes, Eucerinodina and Eucerina, relegating the former Eucerinodini to subtribal status.

Canephorula falls easily within the Eucerina and therefore the tribe Canephorulini vanishes.

The genera of Emphorini are consistently grouped, with *Ancyloscelis* as sister to the others. Placement of *Ancyloscelis* in the Emphorini was suggested earlier by J. S. Moure (in litt.). It is different enough from other Emphorini that we propose subtribal status for it, the Ancyloscelina new subtribe, as distinguished from Emphorina.

The Ctenoplectrini, the remarkable features of which led to its recognition as a distinct family (e.g., Michener and Greenberg, 1980), is a tribe of Apinae. The characters that led Michener and Greenberg to place the Ctenoplectridae as the sister group to all L-T bees are now recognized as reversals in the mouthparts toward S-T bee characteristics (see Introduction; also Silveira, in press).

The Tapinotaspini is a new family-group name for a distinctive group of genera formerly included in Exomalopsini. These genera are those of sections 1, 2, and 5 of Exomalopsini as understood by Michener and Moure (1957); in that work the relationship of these three sections was recognized. The proposed relationships of *Caenonomada* to Centridini, Rhathymini and Ericrocidini (Snelling and Brooks, 1985) and of *Monoeca* to Centridini (Neff and Simpson, 1981) are not supported.

CONCLUDING REMARKS

Our work was based on exemplars of a limited list of genera. Familiarity with other species and other genera suggests to us that most of the character states that we recorded apply also to the relatives of each exemplar. But we know of cases in which this is not true for certain characters, and there are doubtless many more such cases. Each group needs to be more broadly examined to clarify such matters. Moreover, each group needs to be reanalyzed not only to include genera and species that we did not study in detail, but to re-evaluate the characters that we did use.

Among the difficulties in a study of a large group such as the L-T bees are selection of synapomorphic characters and coding of their states. One would bias the results unduly toward the prior classification by using only those characters already known to distinguish recognized taxa; in L-T bees another problem resulting from such a policy would be too few characters for a reasonable analysis. We therefore used as many polarizable characters as we could find that were not autapomorphic at the level of our exemplars. Many of these characters had low consistency indices, reversing and rereversing, or a given state appearing to have evolved repeatedly among diverse taxa. These characters, however, may be phylogenetically important within smaller groups, such as a tribe. Homologies can be more certainly appraised within such a group. For such a study the polarity of some characters may be altered relative to our study; our polarization was for L-T bees as a whole but for analysis of a smaller group such as a tribe, polarity should be determined on the basis of outgroups for that tribe. We hope our results will help in selecting such outgroups. Users of our work for this purpose should note, however, that certain nodes (we list the worst above) are weak; outgroups should be selected as though these nodes were polytomies even though they may be supported in consensus trees. When levels of homoplasy are high, as they were in this study, minimum-length trees based on parsimony may be extremely unstable in the face of additional characters or taxa, so that weak nodes should never be taken too seriously. As indicated in the section on Classificatory Results, we here report reanalyses, with additional characters and repolarizations as necessary, for the tribes of Xylocopinae and Nomadinae. Moreover Silveira (1993) has made such a reanalysis of the Apinae.

Some preliminary biogeographical comments based on the distributions of the 41 terminal suprageneric taxa of L-T bees are now possible. The numbers of such taxa in major biogeographical regions are as follows: neotropical 29, nearctic 25, palearctic 20, subsaharan Africa 17, oriental 16 and Australia including New Guinea 11. In general these numbers are correlated with the climatic and ecological diversity of the areas. The neotropical region has the greatest number of taxa. Its great importance for bee taxa is further shown by the fact that it is the area of maximum diversity for several widespread taxa: Lithurgini, Epeolini, and Meliponini. The neotropical region also has the greatest climatic diversity—tropical forest, savanna, southern temperate areas, mountains, deserts, etc. North America has great diversity but the North American tropics are placed in the neotropical region; if one excludes basically neotropical taxa that range into the southern nearctic, there are only 20 nearctic taxa.

Of greater interest are the possible contributions of distributional patterns to our knowledge of antiquity of taxa. Fourteen of the taxa are restricted to the neotropical region or are basically neotropical but extend north only into the southwestern nearctic region. Absence of these taxa from Africa suggests that they are probably of more recent origin than the full separation of South America and Africa; it was probably Eocene or later before the Atlantic was wide enough to form a long-term barrier for flying insects like bees.

Two pairs of tribes, each of which may owe its duality to the long isolation of South America after its separation from Africa, are the Anthophorini-Centridini and the Melectini-Ericrocidini. (The sister-group relationship of Anthophorini and Centridini is by no means certain.) In each case the first listed tribe is widely distributed but scarce or (for Melectini) absent in South America, while the second is principally South American, although ranging north in reduced diversity into the southwestern United States. These tribes are therefore likely to be younger than the separation of Africa and South America. These pairs are not independent; the Melectini are cleptoparasites of Anthophorini, the Ericrocidini, of Centridini.

The Fideliini, a relict group now found in desertic areas of southern Africa, with one species of *Fidelia* in Morocco and the genus *Neofidelia* in central Chile, may once have been

widespread, or an old, limited distribution may have been divided by the spreading Atlantic Ocean.

The pantropical Meliponini, which occurred as far north as the Baltic region in late Eocene times and as New Jersey in late Cretaceous, probably owes its wide distribution to its antiquity. Nonetheless, no genera are the same on both sides of the Atlantic Ocean (Michener, 1990c) although *Trigona* occurs both in the neotropics and in the Indoaustralian region; the genera are probably more recent than the Atlantic.

For the majority of bee family-group taxa, fossil evidence is totally lacking. Fossils of Meliponini are mentioned above; for comments on the reliability of the late Cretaceous date for *Trigona,* see Rasnitsyn and Michener (1991). Otherwise, among L-T bees, the apine clade has well-preserved and identifiable fossil species as old as the Eocene (Zeuner and Manning, 1976); forms assigned to the Ctenoplectrini may be misplaced.

There is not even a tendency for old taxa (as judged by the fossil record) to be near the bases of the cladograms. Of course the fossil record is extremely fragmentary and biased toward taxa that collect resin for nesting purposes and thus occasionally are trapped in it and fossilized in amber. The fragmentary record that we have, however, and the fact that bee evolution may not have begun until the rise of the angiosperms in the early Cretaceous, suggest that there may have been a rapid early radiation, followed by relative stasis in some clades. Families well represented in Australia are S-T bees (Colletidae, Stenotritidae, and Halictidae) and the Colletinae show congeneric relationships to South American forms. Therefore the major radiation of S-T bees, at least the Colletinae, presumably preceded the interruption of the Australian-South American biotic exchange through Antarctica.

There are no family-group taxa of L-T bees limited to or highly diversified in Australia. Therefore L-T bees there are relatively recent arrivals, and L-T bees as a group must be more recent, at least in the southern hemisphere, than the time when Australia became isolated from other land masses. Thus the major early radiation of L-T bees either postdated that time or possibly was in other parts of the world.

Appendix: NUMBER OF TUBULES IN REPRODUCTIVE ORGANS

The number of ovarioles per ovary and of sperm tubules per testis (Character 131) is one of the strongest characters for separating families of L-T bees. Of course dissections have not been made for all genera; exceptions may yet be found. Based on the literature and our own dissections, the numbers are the same for ovaries and testes, and are three for S-T bees and megachilids, four for Apidae except that in *Apis* and some parasitic groups (Nomadinae, *Ericrocis*) there are even more. This statement is based in part on the literature (Alexander and Rozen, 1987; Iwata, 1955; Iwata and Sakagami, 1966; Rozen, 1986; Rozen and Roig-Alsina, 1991 and numerous works on halictid and allodapine bee life histories and social biology, in which ovarian development has been routinely examined, and number of ovarioles incidentally reported or illustrated; see citations in Michener, 1974, 1990a, b). In addition the results of new dissections are listed below:

Females, number of ovarioles per ovary: *Manuelia gayatina* (Spinola), 4; *Ancyloscelis apiformis* (Fabricius), 4.

Males, number of tubules per testis: *Hesperapis carinata* Stevens, 3; *Anthidium porterae* Cockerell, 3; *Megachile mendica* Cresson, 3; *Megachile petulans* Cresson, 3; *Xylocopa virginica* (Linnaeus), 4; *Ceratina calcarata* Robertson, 4; *Triepeolus distinctus* Cresson, 5; *Bombus pennsylvanicus* (DeGeer), 4; *Bombus bimaculatus* Cresson, 4; *Euglossa viridissima* Friese, 4; *Exomalopsis pygmaea* (Cresson), 4; *Paratetrapedia* sp., 4; *Ptilothrix bombiformis* (Cresson), 4; *Diadasia baeri* (Vachal), 4; *Melissodes agilis* Cresson, 4; *Svastra obliqua* (Say), 4; *Peponapis pruinosa* (Say), 4; *Anthophora walshii* Cresson, 4; *Habropoda pallida* (Timberlake), 4; *Centris atripes* Mocsáry, 4.

LITERATURE CITED

Alexander, B. 1990. A cladistic analysis of the nomadine bees. Systematic Entomology 15: 121-152.

Alexander, B., and J. G. Rozen, Jr. 1987. Ovaries, ovarioles and oocytes in parasitic bees. Pan-Pacific Entomologist 63: 155-164.

Ashmead, W. H. 1899. Classification of the bees, or the superfamily Apoidea. Transactions of the American Entomological Society 26: 49-100.

Börner, C. 1919. Stammesgeschichte der Hautflügler. Biologisches Zentralblatt 39: 145-186.

Brooks, R. W. 1988. Systematics and phylogeny of the anthophorine bees. University of Kansas Science Bulletin 53: 436-575.

Brothers, D. J. 1975. Phylogeny and classification of the aculeate Hymenoptera, with special reference to Mutillidae. University of Kansas Science Bulletin 50: 483-649.

Cameron, S. 1991. A new tribal phylogeny of the Apidae inferred from mitochondrial DNA sequences. Pp. 71-87 *in* D. R. Smith (ed.), Diversity in the Genus *Apis*. Boulder, Colorado: Westview Press.

Cane, J. H. 1979. The hind tibiotarsal and tibial spur articulations in bees. Journal of the Kansas Entomological Society 52: 123-137.

Cresson, E. T. 1887. Synopsis of the families and genera of the Hymenoptera of America, north of Mexico. Transactions of the American Entomological Society, Suppl. Vol.: i-iv + 1-154.

Ehrenfeld, J., and J. G. Rozen, Jr. 1977. The cuckoo bee genus *Kelita,* its systematics, biology, and larvae. American Museum Novitates no. 2631: 1-24.

Farris, J. S. 1969. A successive approximations approach to character weighting. Systematic Zoology 18: 374-385.

Farris, J. S. 1988. Hennig86: Version 1.5. Port Jefferson Station, N. Y.: distributed by the author.

Iwata, K. 1955. The comparative anatomy of the ovary in Hymenoptera. Part I. Aculeata. Mushi 29: 17-34.

Iwata, K., and S. F. Sakagami. 1966. Gigantism and dwarfism in bee eggs in relation to the modes of life, with notes on the number of ovarioles. Japanese Journal of Ecology 16: 4-16.

Jander, R. 1976. Grooming and pollen manipulation in bees (Apoidea): The nature and evolution of movements involving the foreleg. Physiological Entomology 1: 179-194.

Kirby, W. 1802. Monographia Apum Angliae. Vol. 1, xxii + 258 pp.; vol. 2, 338 pp. + 18 pls. Ipswich.

Laroca, S., C. D. Michener and R. M. Hofmeister. 1989. Long mouthparts among "short-tongued" bees and the fine structure of the labium in *Niltonia*. Journal of the Kansas Entomological Society 62: 400-410.

Latreille, P. A. 1802. Histoire Naturelle des Fourmis. xvi + 445 pp, 12 pls. Paris.

Lepeletier de Saint-Fargeau, A. 1836, 1841. Histoire Naturelle des Insectes—Hyménoptères. Vol. 1, 547 pp.; vol. 2, 680 pp. Paris.

Maddison, D. R. 1991. The discovery and importance of multiple islands of most-parsimonious trees. Systematic Zoology 40: 315-328.

McGinley. R. J. 1981. Systematics of the Colletidae based on mature larvae with phenetic analysis of apoid larvae. University of California Publications in Entomology 91: i-xvi + 1-307.

McGinley, R. J., and J. G. Rozen, Jr. 1987. Nesting biology, immature states, and phylogenetic placement of the palearctic bee *Pararhophites*. American Museum Novitates no. 2903: 1-21.

Michener, C. D. 1944. Comparative external morphology, phylogeny, and a classification of the bees. Bulletin of the American Museum of Natural History 82: 151-326.

Michener, C. D. 1953. Comparative morphological and systematic studies of bee larvae with a key to the families of hymenopterous larvae. University of Kansas Science Bulletin 35: 987-1102.

Michener, C. D. 1965. A classification of the bees of the Australian and South Pacific regions. Bulletin of the American Museum of Natural History 130: 1-362, pls. 1-15.

Michener, C. D. 1970. Social parasites among African allodapine bees. Zoological Journal of the Linnean Society [London] 49: 199-215.

Michener, C. D. 1974. The Social Behavior of the Bees: A Comparative Study. i-xii + 1-404 pp. Cambridge, Massachusetts: Harvard University Press.

Michener, C. D. 1975. A taxonomic study of African allodapine bees. Bulletin of the American Museum of Natural History 155: 67-240.

Michener, C. D. 1979. Biogeography of the bees. Annals of the Missouri Botanical Garden 66: 277-347.

Michener, C. D. 1981. Classification of the bee family Melittidae with a review of species of Meganomiinae. Contributions of the American Entomological Institute 18(3): i-iii + 1-135.

Michener, C. D. 1983. The classification of the Lithurginae. Pan-Pacific Entomologist 59: 176-187.

Michener, C. D. 1985. A comparative study of the mentum and lorum of bees. Journal of the Kansas Entomological Society 57(for 1984): 705-714.

Michener, C. D. 1990a. Reproduction and caste in social halictine bees. Pp. 77-121 *in* W. Engels (ed.), Social Insects—An Evolutionary Approach to Castes and Reproduction. Berlin: Springer-Verlag.

Michener, C. D. 1990b. Castes in xylocopine bees. Pp. 123-146 *in* W. Engels (ed.), Social Insects—An Evolutionary Approach to Castes and Reproduction. Berlin: Springer-Verlag.

Michener, C. D. 1990c. Classification of the Apidae. University of Kansas Science Bulletin 54: 75-164.

Michener, C. D., and R. W. Brooks. 1984. Comparative study of the glossae of bees. Contributions of the American Entomological Institute 22(1): i-iii + 1-73.

Michener, C. D., and A. Fraser. 1978. A comparative anatomical study of mandibular structure in bees. University of Kansas Science Bulletin 51: 463-482.

Michener, C. D., and L. Greenberg. 1980. Ctenoplectridae and the origin of long-tongued bees. Zoological Journal of the Linnean Society [London] 69: 183-203.

Michener, C. D., and J. S. Moure. 1957. A study of the classification of the more primitive non-parasitic anthophorine bees. Bulletin of the American Museum of Natural History 112: 395-451.

Neff, J. L., and B. B. Simpson. 1981. Oil-collecting structures in the Anthophoridae (Hymenoptera): Morphology, function, and use in systematics. Journal of the Kansas Entomological Society 54: 95-123.

Plant, J., and H. F. Paulus. 1987. Comparative morphology of the postmentum of bees (Hymenoptera: Apoidea) with special remarks on the evolution of the lorum. Zeitschrift fur Zoologische Systematik und Evolutionsforschung 25: 81-103.

Popov, V. V. 1949. Tribe Pararhophitini (Hymenoptera, Anthophorinae) as an early Tertiary element of the contemporary fauna of the desert in Central Asia and Egypt. Doklady Akademii Nauk SSSR 66: 507-510 [in Russian].

Prentice, M. 1991. Morphological analysis of the tribes of Apidae. Pp. 51-69 *in* D. R. Smith (ed.), Diversity in the Genus *Apis*. Boulder, Colorado: Westview Press.

Rasnitzyn, A. P., and C. D. Michener. 1991. Miocene fossil bumble bee from the Soviet far east with comments on the chronology and distribution of fossil bees. Annals of the Entomological Society of America 84: 583-589.

Robertson, C. 1904. Synopsis of Anthophila. Canadian Entomologist 36: 37-43.

Roig-Alsina, A. 1989. The tribe Osirini, its scope, classification, and revisions of the genera *Parepeolus* and *Osirinus*. University of Kansas Science Bulletin 54: 1-23.

Roig-Alsina, A. 1990. *Coelioxoides* Cresson, a parasitic genus of Tetrapediini. Journal of the Kansas Entomological Society 63: 279-287.

Roig-Alsina, A. 1991. Cladistic analyses of the Nomadinae s. str. with description of a new genus. Journal of the Kansas Entomological Society 64: 23-37.

Rozen, J. G., Jr. 1977. The ethology and systematic relationships of fideliine bees, including a description of the mature larva of *Parafidelia*. American Museum Novitates no. 2637: 1-15.

Rozen, J. R., Jr. 1986. Survey of the number of ovarioles in various taxa of bees. Proceedings of the Entomological Society of Washington 88: 707-710.

Rozen, J. R., Jr. 1987. Nesting biology of the bee *Ashmeadiella holtii* and its cleptoparasite, a new species of *Stelis*. American Museum Novitates no. 2900: 1-10.

Rozen, J. G., Jr. 1991. Biology and larvae of the cleptoparasitic bee *Townsendiella pulchra* and nesting biology of its host, *Hesperapis larreae*. American Museum Novitates no. 3005: 1-11.

Rozen, J. G., Jr., K. R. Eickwort and G. C. Eickwort. 1978. The bionomics and immature stages of the cleptoparasitic bee genus *Protepeolus*. American Museum Novitates no. 2640: 1-24.

Rozen, J. G., Jr., and C. D. Michener. 1988. Nests and immature stages of the bee *Paratetrapedia swainsonae*. American Museum Novitates no. 2909: 1-13.

Rozen, J. G., Jr., and A. Roig-Alsina. 1991. Biology, larvae, and oocytes of the parasitic bee tribe Caenoprosopidini. American Museum Novitates no. 3004: 1-10.

Sakagami, S. F., and C. D. Michener. 1987. Tribes of Xylocopinae and origin of Apidae. Annals of the Entomological Society of America 80: 439-450.

Schenck, A. 1859. Beschreibung Nassauischer Bienenarten. Jahrbucher des Vereins für Naturkunde im Herzogthum Nassau 14: 1-414.

Schenck, A. 1869. Beschreibung Nassauischen Bienen, Zweiter Nachtrag. Jahrbucher Nassau des Vereins für Naturkunde 21-22: 269-382.

Schmiedeknecht, O. 1882. Apidae Europaeae. Vol. 1, xiii + 383 pp. Berlin.

Schönitzer, K. 1986. Comparative morphology of the antenna cleaner in bees. Zeitschrift für Zoologische Systematik und Evolutionsforschung 24: 35-51.

Schönitzer, K., and M. Renner. 1980. Morphologie der Antennenputzapparate bei Apoidea. Apidologie 11: 113-130.

Sheppard, W. S. and B. A. McPherson. 1991. Ribosomal DNA diversity in Apidae. Pp. 87-102 *in* D. R. Smith (ed.), Diversity in the Genus *Apis*. Boulder, Colorado: Westview Press.

Silveira, F. A. 1993. Phylogenetic relationships of Exomalopsini and Ancylini. University of Kansas Science Bulletin 55: 163-173.

Silveira, F. A. In press. The mouthparts of *Ancyla* and the reduction of the labiomaxillary complex among long-tongued bees. Entomologica Scandinavica.

Smith, F. 1853. Catalogue of Hymenopterous Insects in the Collection of the British Museum, Part 1, [i] + 1 + 197 pp., 6 pls. London.

Snelling, R. R., and R. W. Brooks. 1985. A review of the genera of cleptoparasitic bees of the tribe Ericrocini. Contributions in Science, Natural History Museum of Los Angeles County, no. 369: 1-34.

Snodgrass, R. E. 1956. Anatomy of the Honey Bee. Ithaca, New York: Cornell University Press. i-xiv + 1-334 pp.

Sŭstera, O. 1958. Übersicht des Systems der paläarktischen und mitteleuropäischen Gattungen der Superfamilie Apoidea. Acta Entomologica Musei Nationalis Prague 32: 443-463.

Swofford, D. L. 1990. Phenetic Analysis Using Parsimony, Version 3.0g. Champaign, Illinois: Illinois Natural History Survey.

Tkalcŭ, B. 1972, 1974. Arguments contre l'interprétation traditionnelle de la phylogénie des abeilles. Bulletin de la Société Entomologique de Mulhouse, Apr.-June 1972: 17-28; Apr.-June 1974: 17-40.

Thomson, C. G. 1872. Skandenaviens Hymenoptera, vol. 2, pp. 1-286. Lund.

Warncke, K. 1977. Ideen zum natürlichen System der Bienen. Mitteilungen Münchner Entomologischen Gesellschaft 67: 39-63.

Warncke, K. 1979. Beiträge zur Bienenfauna des Iran: 10. Die Gattung *Ancyla* Lep., mit einer Revision der Bienengattung *Ancyla* Lep. Bollettino del Museo Civico di Storia Naturale di Venezia 30: 183-195.

Whitfield, J. B. 1992. Phylogeny of the non-aculeate Apocrita and the evolution of parasitism in the Hymenoptera. Journal of Hymenoptera Research 1: 3-14.

Winston, M. L. 1979. The proboscis of the long-tongued bees: A comparative study. University of Kansas Science Bulletin 51: 631-667.

Zeuner, F. E., and F. J. Manning. 1976. A monograph on fossil bees. Bulletin of the British Museum (Natural History), Geology 27: 149-268, pls. 1-4.

Phylogenetic Relationships of the Exomalopsini and Ancylini (Hymenoptera: Apoidea)[1]

FERNANDO A. SILVEIRA[2]

ABSTRACT

A phylogenetic definition of Exomalopsini and Ancylini and an understanding of their phylogenetic position among the Apinae (sensu Roig-Alsina & Michener) is attempted through a parsimony analysis of data modified from Roig-Alsina & Michener (1993). The monophyly of each of those tribes and their sister-group relationship are suggested, but could not be demonstrated unequivocally. They apparently constitute, with the tribes Emphorini, Tapinotaspini and Eucerini, a clade ("eucerine line") within the Apinae. A clade composed of the tribes Apini, Meliponini, Bombini, Euglossini, Centridini and Anthophorini ("apine line") is also supported. In many of the trees obtained, Tetrapediini was the most primitive branch of the Apinae, and Ctenoplectrini was part of the "eucerine line"; in other trees, these two tribes were the basal branches of the "apine line". More studies, employing new sets of characters, may clarify the relations among the tribes of the Apinae.

INTRODUCTION

The tribe Exomalopsini was erected by Michener (1944) to group what he considered to be the most primitive non-parasitic anthophorine bees. It was redefined by Michener & Moure (1957) as being composed of 11 genera in 5 sections: 1. *Ancyloscelis;* 2. *Caenonomada;* 3. *Monoeca;* 4. *Exomalopsis, Isomalopsis, Teratognatha* and *Eremapis* and 5. *Chalepogenus, Lanthanomelissa, Tapinotaspis* and *Paratetrapedia.* Later, a new genus, *Chilimalopsis,* was added by Toro (1976) and said to be allied to *Exomalopsis.* In a recent phylogenetic study of the long-tongued bees, Roig-Alsina & Michener (1993) removed all but group 4 from Exomalopsini.

Thus defined, Exomalopsini is American, with its center of abundance and diversity in southern South America. It was in this continent, according to Michener (1944), that the group developed from ancestral stocks isolated during the Tertiary.

The Palearctic genera *Pararhophites, Ancyla* and *Tarsalia* have been said to be related to, or to belong to Exomalopsini (Michener, 1944, 1979; Michener & Moure, 1957). The tribe Pararhophitini was erected by Popov (1949) for *Pararhophites,* which was later (McGinley & Rozen, 1987; Roig-Alsina & Michener, 1993) demonstrated to be part of the megachilid lineage. *Ancyla* and *Tarsalia* were grouped in the Ancylini by Michener (1944). This systematic arrangement has been generally accepted and the question remained whether or not Ancylini was allied to or a synonym of Exomalopsini (e.g. Popov, 1949; Michener & Moure, 1957; Michener, 1979; McGinley & Rozen, 1987). Warncke (1977, 1979) pointed out that *Ancyla* is equipped with short mouthparts, and stated that this genus is a link between the families Melittidae and Anthophoridae. In fact, from the time it was erected by Lepeletier (1841) until 1944, *Ancyla* was always placed among the short-tongued bees (e.g. Dalla Torre & Friese, 1895; Dalla Torre, 1896; Ashmead, 1899). However, Warncke considered the long-tongued *Tarsalia* to be a subgenus of *Ancyla.* Roig-Alsina & Michener (1993) suggested that Ancylini would probably be a basal branch of the Eucerini, but since only *Tarsalia* was examined, and in the absence of strong evidence, they preferred to keep Ancylini as a separate tribe.

For the present study, character states of *Ancyla* were added to the data of Roig-Alsina & Michener which were then re-analyzed, in an attempt to provide new insight on the phylogenetic definition of the Exomalopsini and of the Ancylini, and to improve our understanding of the relationships between these two tribes and the other tribes of the Apinae as redefined by Roig-Alsina & Michener (1993).

ACKNOWLEDGMENTS

I wish to thank Jerome G. Rozen, Jr. and the American Museum of Natural History for the loan of specimens of *Ancyla;* Charles D. Michener, Arturo Roig-Alsina & Byron A. Alexander, of the Snow Entomological Museum of the University of Kansas, for help in the interpretation of characters, dissection of specimens and discussion of this paper. J. S. Ashe, also from the Snow Museum, is acknowledged for valuable opinions on cladistic analysis and D. Yanega and R. Constantino for helping in the elaboration of the cladograms. This paper was produced with the support of a scholarship granted by the National Council for Scientific and Technological Development (CNPq) of the Brazilian Ministry of Science and Technology.

---

[1]CONTRIBUTION NO.3102 FROM THE SNOW ENTOMOLOGICAL MUSEUM, UNIVERSITY OF KANSAS, LAWRENCE.

[2]DEPARTMENT OF ENTOMOLOGY AND SNOW ENTOMOLOGICAL MUSEUM, SNOW HALL, UNIVERSITY OF KANSAS, LAWRENCE, KANSAS 66045-2119, U.S.A.

MATERIAL AND METHODS

Throughout this paper, names of taxa will be used according to the classification proposed by Roig-Alsina & Michener (1993), except where otherwise stated, and that paper will be referred to as Roig-Alsina & Michener.

The *Ancyla* examined were one female and two males, identified by J. Bequaert as *A.oraniensis* Lepeletier, and a male *Ancyla* sp. They agree with the generic and specific descriptions by Lepeletier (1841). The only internal features examined for *Ancyla* were those in the head that could be observed through the proboscidial fossa of the female, whose mouthparts had been removed for study. The other internal characters used by Roig-Alsina & Michener were coded as unknown.

Descriptions of the characters employed here are to be found in Roig-Alsina & Michener and will not be repeated. To make results easy to compare with their paper, numbers used here are those of Roig-Alsina & Michener.

Phylogenetic analyses were performed using the program Hennig86 version 1.5 (Farris, 1988 - provided by B. Alexander) in a Zenith Z-386/33E computer with 8 Megabytes of RAM, except for the analyses including Nomadinae, which were performed with an IBM compatible computer with a Cx486DLC processor and 8 Megabytes of RAM. The basic matrix employed was that used by Roig-Alsina & Michener in their analysis "D" (adult morphology, parasitic genera excluded — 55 taxa, 131 characters), to which *Ancyla oraniensis* was added. This matrix was chosen because there are no data available on larval features of *Ancyla* and *Tarsalia*, and to avoid the problems encountered by Roig-Alsina & Michener when trying to analyze parasitic and pollen-collecting bees together. Since Nomadinae is one of the possible sister-groups of Apinae, it was included in some analyses, as explained below.

The following analyses were performed:

Analyses 1A. With the basic matrix described above, the m* and bb* commands (defined in Farris, 1988) were used, with all characters being taken as unordered.

Analysis 1B. Procedures of Analysis 1A were repeated after the character states of the 13 nomadine genera employed by Roig-Alsina & Michener were added to the basic matrix.

Analysis 2. *Ancyla* and *Tarsalia* consistently appeared in the Apinae (sensu Roig-Alsina & Michener) in Analyses 1A and 1B. Consequently, the matrix was reduced in size by replacing Melittidae, Megachilidae and Xylocopinae with an outgroup vector (outgroup-1 in Table 1). The characters for this vector were determined according to the procedures provided by Maddison et al. (1984), based on the topology of Roig-Alsina & Michener's Cladogram 3. Additional modifications were made to the basic matrix as follows: To accomodate *Ancyla*, Character 48 was split into two characters:

48a. Labial palpal segments 1 and 2: (0) Not particularly flattened. (1) Flattened.

48b. Labial palpal segments 1 and 2: (0) Similar in length to segments 3 and 4. (1) Greatly elongated compared to segments 3 and 4.

All bees except *Ancyla* were coded either 0 or 1 for both 48a and 48b. Ancyla has segments 1 and 2 flattened, but similar in length to segments 3 and 4 (Silveira, in press), and thus was coded 1 and 0 for Characters 48a and 48b respectively.

After re-examination of the specimen, Character 56 was coded for *Tarsalia* as 56-1 (it was coded by Roig-Alsina & Michener as 56-0). Characters 7, 9, 15, 18, 19, 25, 26, 31, 34, 42, 57, 59, 108, 111, 112, 114, 115, 117 and 129 did not show any variation among the Apinae and were therefore excluded. The matrix obtained after all these modifications is shown in Table 1.

Analysis 2A was made with the above described matrix, using the m* and bb* procedures of Hennig86 with the characters unordered.

Analysis 2B was made by applying successive weighting (Farris,1969) in the results of Analysis 2A.

Analysis 3A. The same procedures as for Analysis 2A were repeated, but here Nomadinae was considered as the sister group of the Apinae when the outgroup vector was defined (outgroup-2 in Table 1). An outgroup vector for the Nomadinae was constructed using the topology obtained by Roig-Alsina & Michener in their reanalysis of this subfamily (see their "Classificatory Results"). This outgroup vector was then used to construct the outgroup vector for the Apinae, along with the outgroup vectors for Melittidae, Megachilidae and Xylocopinae.

Analysis 3B was made applying successive weighting to the results of Analysis 3A.

Analysis 4. Parsimony analyses were made to study the relationships among the tribes Eucerini, Tapinotaspini, Emphorini, Exomalopsini and Ancylini, which in several of the trees obtained in the previous analyses appeared to constitute a monophyletic group, the "eucerine line." The tribes Tetrapediini and Ctenoplectrini, the "apine line" (composed of the tribes Apini, Meliponini, Bombini, Euglossini, Centridini and Anthophorini) and the outgroup vector employed in the previous analyses were used as outgroups to construct a new outgroup vector.

Analysis 4A was made using the phylogenetic hypothesis for the outgroups exemplified by Fig. 7a for character optimization.

Analysis 4B was made using the phylogenetic hypothesis of Fig. 8a for character optimization.

The relationships among taxa are frequently presented below by means of consensus trees in which genera belonging to monophyletic groups were collapsed. These trees (which I am naming "summaries of consensus trees") appear fully resolved when polytomies are restricted to the relationships among genera within monophyletic tribes.

Abbreviations used in explaining the phylogenetic analysis are: L = tree length, ci = consistency index and ri = retention index.

TABLE 1. Data matrix for the parsimony analyses of the Apinae (analyses 2 and 3). Character numbers are the ones used by Roig-Alsina & Michener (1993). Outgroup-1 includes Melittidae, Megachilidae and Xylocopinae; Outgroup-2 Includes these plus Nomadinae.

	CHARACTER NUMBERS
	1111111111111111111111111
	1111111222222223333333344444444445555555566666666667777777777888888888999999999900000000011111222222223
TAXA	1234568012346701234789023567890134567889012345680123456789012345678901234567890123456789012345679036890123456780
Outgroup-1	0000100?000000001O?1O?0001?001?1?0100110011207100O?00000?0000102100110O0?0000?01000000?0??01O?000?10?0???0012?00?
Outgroup-2	00001???000000021O?1O?0001000111001001100112001000000000?0000102100010001000000100000000?0010?0000100010?0?21000?
Eremapis	0021111000002002002010110010001110010011101120010000000001000000110001000000001010000000001010000010020001010210O?
Teratogna	0020111000020020020101100100001100100111011200110000000010000001100012000000020100021000000100000000100101021101?
Isomalops	0020111000010120020101100100001100100111011200100010000001010000110010200000002010002100000100000000010011101021001?
Exomalops	0020101000000001012010110010000110010011101120010001000001011000110010100000002010002100000100000000100210102100l
Tapinotas	0020101000020021110101110100001100100111011200110011000010111102000102100000021100011000001102000100000210102120?
Tapinorhi	0000101000020021020101110100001100101111011200110011000010111102100102100000021100011000000101000000002101021201?
Arhysoceb	0010111000020021020101110110001100100111011200110011000020111112100101100000021100021000000201000000200210102120?
Paratetra	0011111000020020020101110110001100100111011201100110000020111112100102000000011000021000000201000000200210102120l
Monoeca	0010101000020022020101100110001100100111011200110011000010101111100101100000011211210000002010000000021010212O?
Caenonomad	0010101000020022020101110100001100100111011211100001000021121102100102100000021010001010000202010000000210102120?
Ancyloscel	0011111100210220201011001000011001011100112001100100001100101121000010000000201000010000001000000002002101121001
Melitoma	0010111010011022021101111100l?110010011001120011001000011012011210010200000002010000000000100000000210210102120?
Diadasia	0010111010021020020101111110000110010111001120011001000011012010210010200000002010000000000100000000210210102120l
Diadasina	0010111010021020020101111100l?111010111101200100010000110111012100102000000010100000000000100000000210210102120?
Ptilothryx	0000111010021020020101111100l?111010111001120011001000011012011210011200000001010000001000010000000210210102120l
Tetrapedia	0000111000010020110101100110011100100111011200100010000010120102100100120000002110011010000102010000211010012001?
Ancyla	0000100000020000??0101100100011200100101000200100010?00???00000?1?00?100000002000001100000201000000000201202100?
Tarsalia	00?0101100020022020101100110001101100111111201000011000?1?10000?1?0101000000020100011000000221000000210011202100?
Eucerinoda	0010101101O?00?2020101100100001100100111012101100l0?00?1?10000?1?0102000000021100011000000101000000200210202100?
Canephorul	0111101101011021020101100011001100100111012001200100000100001021001000001000211000011100101200000000000102021102
Eucera	0011101101010022020101100101001100101111012012001100001101010210010200000002210001100010012100100000001020211O1
Melissodes	0011101101010022020101100100001100100111011210120011000010100102100102000000022100011000000220001000000210202110l
Svastra	0011101101010022020101100101001100101111012012001100001011010210010200000002110001100000012000100000001020210O1
Peponapis	0011111101011022020101100101011100101111012012001100001111010210010200000002210000100000012000100000021020211O1
Anthophora	0010111000000022020111100100002011001111012001000001000200001131101000000002100000200001122110000021010002000l
Habropoda	0010111000000122020111100000000200100110111O?0100000100020000113110100000000021000002000010211100000201010022000l
Deltoptila	1110111000000022021111000100000200100110111211100000100010000113110100000000022000002000010211000000211010121000?
Centris	0000101000000020010101100100000101100110111210100010100010010113100110100000011011101010011220000000211010122000l
Epicharis	0000111000010021020101100110000101100110112210100010100011000102100102100000011021112010000221000000001012121100?
Bombus	0000011000010120020101000100010111011011120010100100001001112010111200111101100021010000213000011201010001100l
Apis	0000001000011120120001000100l?01101201100122001011010210100001201011l??2111110110002100000023002001120212001200O2
Melipona	0000001000011120120100000100000110120110112200101101121010011120100l1??2111101110000100020033001001120132000210O1
Partamona	0100001000O?1120120100107100000110120110012200101101121010001120100l1??2111101110000100120030101001120132000210O1
Euglossa	0101111000l?002202110110011000010110011011121110100100001101012210111210111111111000210100002220000112010100011001
Eufriesea	0101111100l?0122011101107110000101100110111211101001000011010122101112101111101110021010000223000011201010001100?
Ctenoplect	0100111000020012010101100000001000000000000200110010100010100?02100100100001011100010010100200000100200210002100?

RESULTS

Analysis 1A (all long-tongued, pollen-collecting bees) was made largely to determine the effect of the addition of *Ancyla* to the results of Roig-Alsina & Michener. It resulted in 1684 most parsimonious trees (+ memory overflow, L = 643, ci = 26, ri = 66). The topology of the consensus tree for this analysis is similar to that obtained by Roig-Alsina & Michener in their analysis "D", and a summary of it is presented in Fig. 1. In Roig-Alsina & Michener's consensus tree, *Exomalopsis* and *Isomalopsis* are involved in a trichotomy with a clade containing all other apine bees, while here *Exomalopsis* arises as a branch subsequent to *Isomalopsis* and as the sister group for all other apine tribes. Also, a clade composed of Ctenoplectrini, Tetrapediini and the apine line (Centridini + Anthophorini + apine clade) is suggested by Analysis 1A.

The number of trees required to reach memory overflow in this analysis (1684) was lower than in the comparable analysis by Roig-Alsina & Michener, which reached overflow at 1712 trees (the same computer was used in both analyses). This may be due to the enlargement of the matrix with the inclusion of *Ancyla* and the splitting of Character 48. It is possible that if more trees had been obtained, new topologies would have been found and that Roig-Alsina & Michener's less resolved consensus tree would have resulted.

Analysis 1B (all pollen-collecting, long-tongued bees plus Nomadinae) yielded 2303 most parsimonious trees (L = 757; ci = 22; ri = 66). The consensus tree for this analysis, a summary of which is presented in Fig. 2, is very similar to the one obtained without Nomadinae. The only noteworthy difference is that Xylocopinae became paraphyletic, with *Xylocopa* and *Manuelia* alternating as the sister group of Apinae in the original cladograms.

Analysis 2A (only pollen-collecting Apinae) yielded 138 minimum-length trees (l = 417, ci = 32, ri = 61). The consensus tree (Fig. 3) is less resolved than the Apinae portion of Roig-Alsina & Michener's consensus tree for their analysis "D" or the consensus trees for Analyses 1A and 1B above. A noteworthy difference is the appearance of Exomalopsini as a monophyletic group.

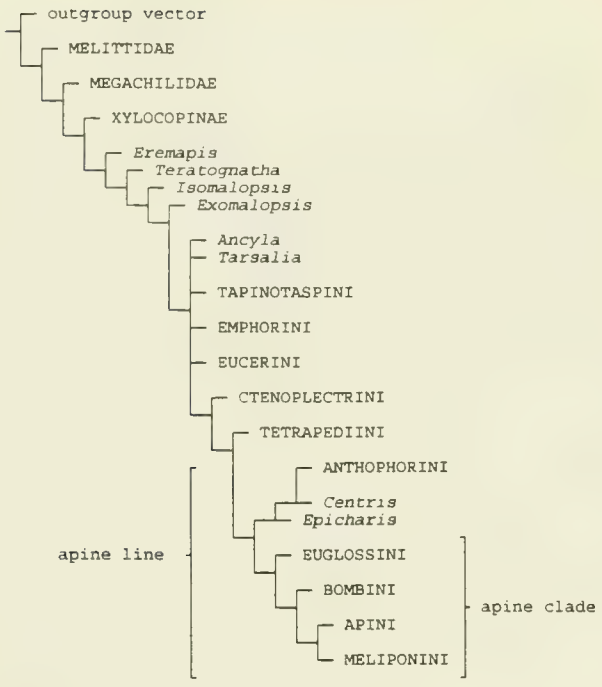


Fig. 1. Summary of the consensus tree for the 1684 shortest trees (length = 643, ci = 26 and ri = 66) obtained in Analysis 1A. Monophyletic groups were collapsed and represented by family, subfamily or tribe names.

Analysis 2B (successive weighting applied to the result of Analysis 2A) yielded three most parsimonious trees (L = 760, ci = 69, ri = 85). The weights applied to each character and a summary of the consensus tree are shown in Fig. 4.

Analysis 3A (only Apinae, Nomadinae included in the outgroup vector) yielded 96 most parsimonious trees (L= 417; ci = 35; ri = 62). The consensus tree for this analysis is exactly equal in topology to the Apinae portion of the trees obtained in Analysis 1B (Fig. 2).

Analysis 3B (successive weighting applied to the result of Analysis 3A), yielded 8 most parsimonious trees (L = 774; ci = 68; ri = 84). The consensus tree for these cladograms (Fig. 5) is very similar to the one obtained for Analysis 2B (Fig. 4), but the topology of the eucerine line is not fully resolved, with Tapinotaspini, Emphorini, Eucerini and Exomalopsini arising from a polytomy. As in Analysis 2B, the Ancylini appears closely related to Exomalopsini. Here, however, in one of the trees *Eremapis* + *Teratognatha* is the first group to branch off of the exomalopsine stem, and *Tarsalia* + *Ancyla* is the sister group of *Isomalopsis* + *Exomalopsis*. In the other 7 trees, *Ancyla* + *Tarsalia* is the sister-group for all of the exomalopsine genera. As a consequence, in the consensus tree, *Ancyla* and *Tarsalia* arise as sister taxa from a polytomy with *Exomalopsis, Isomalopsis* and *Eremapis* + *Teratognatha.*

Analyses 4A and 4B did not result in better resolution of the relations within the "eucerine line". They resulted respectively in 96 trees and 24 trees including all topologies obtained in Analyses 2 and 3.

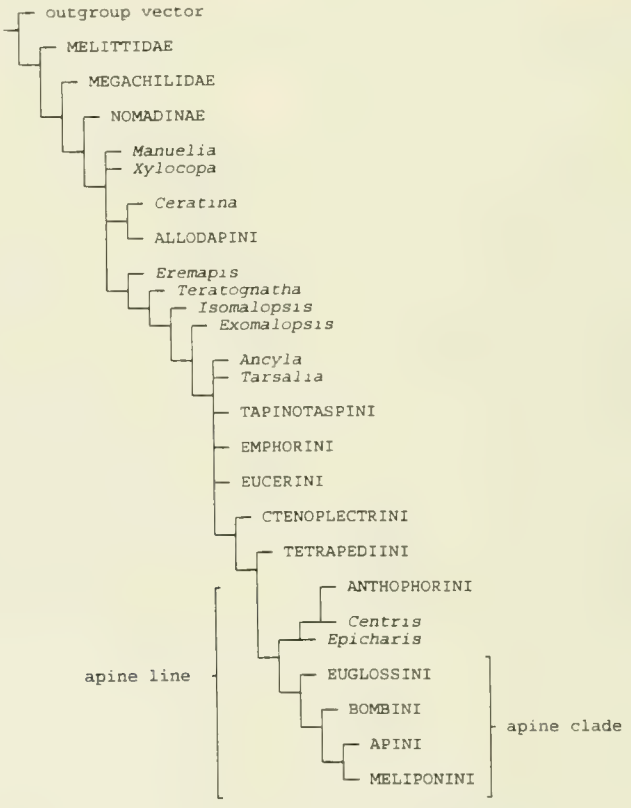


Fig. 2. Summary of the consensus tree for the 2303 shortest trees (length = 757, ci = 22 and ri = 66) obtained in Analysis 1B. Monophyletic groups were collapsed and represented by family, subfamily or tribe names.

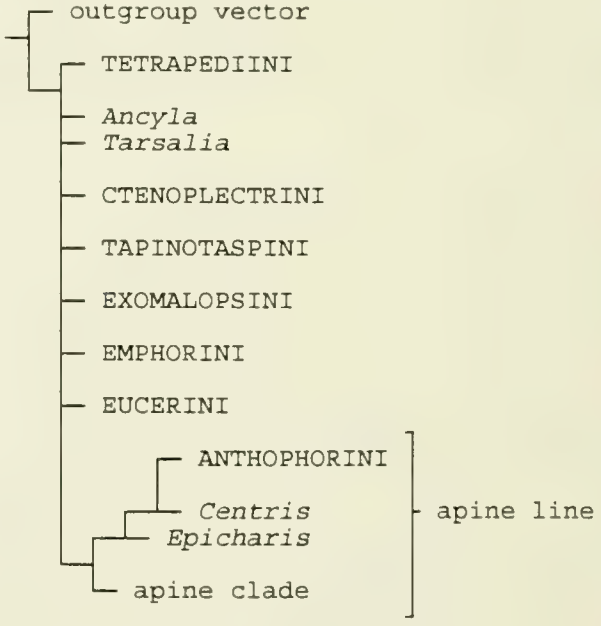
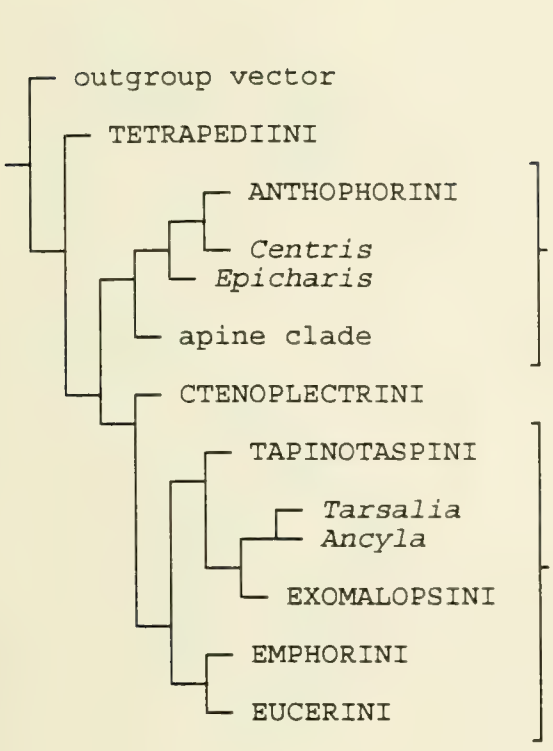


Fig. 3. Summary of the consensus tree for the 138 shortest trees (length = 417, ci = 32, ri = 61) obtained in Analysis 2A. Monophyletic groups were collapsed and represented by family, subfamily or tribe names.

a



b

1	2	3	4	5	6	8	10
10	0	2	1	10	0	0	1
11	**12**	**13**	**14**	**16**	**17**	**20**	**21**
10	10	10	1	1	1	0	0
22	**23**	**24**	**27**	**28**	**29**	**30**	**32**
1	0	1	10	10	10	0	4
33	**35**	**36**	**37**	**38**	**39**	**40**	**41**
10	0	0	3	3	0	10	4
43	**44**	**45**	**46**	**47**	**48a**	**48b**	**49**
4	0	10	10	0	10	0	4
50	**51**	**52**	**53**	**54**	**55**	**56**	**58**
1	0	2	10	0	0	10	2
60	**61**	**62**	**63**	**64**	**65**	**66**	**67**
10	10	1	2	2	10	10	10
68	**69**	**70**	**71**	**72**	**73**	**74**	**75**
3	0	0	0	2	4	2	6
76	**77**	**78**	**79**	**80**	**81**	**82**	**83**
10	10	3	1	1	0	0	3
84	**85**	**86**	**87**	**88**	**89**	**90**	**91**
10	4	10	4	3	0	2	1
92	**93**	**94**	**95**	**96**	**97**	**98**	**99**
0	0	0	0	1	10	0	10
100	**101**	**102**	**103**	**104**	**105**	**106**	**107**
3	1	0	2	2	0	10	1
109	**110**	**113**	**116**	**118**	**119**	**120**	**121**
10	0	4	10	1	1	4	2
122	**123**	**124**	**125**	**126**	**127**	**128**	**130**
10	10	3	2	0	2	3	10
131							
10							

Fig. 4. a. Summary of the consensus tree for the 3 shortest trees (length = 760, ci = 69, ri = 85) obtained in Analysis 2B. Monophyletic groups were collapsed and represented by tribe names. **b.** Weights applied for each character (character numbers in boldface).

Exomalopsini: The monophyly of Exomalopsini is supported by Analyses 2A and 2B and by most trees of analysis 3B. This is the only important difference from the results of Roig-Alsina & Michener. Only two characters support this hypothesis in all of those trees: a broad and ovoid specialized region of the paraocular area with sharp limits and a special layer of underlying tissue (Character 3-2); and perhaps the lower extremity of the metapostnotum with a longitudinal ridge extending to the marginal area of the propodeum (Character 75-1; see Discussion and Conclusions and Figs. 7a,d,e,f,g, 8a and 9a). Different sets of additional characters supported the monophyly of Exomalopsini in different topologies.

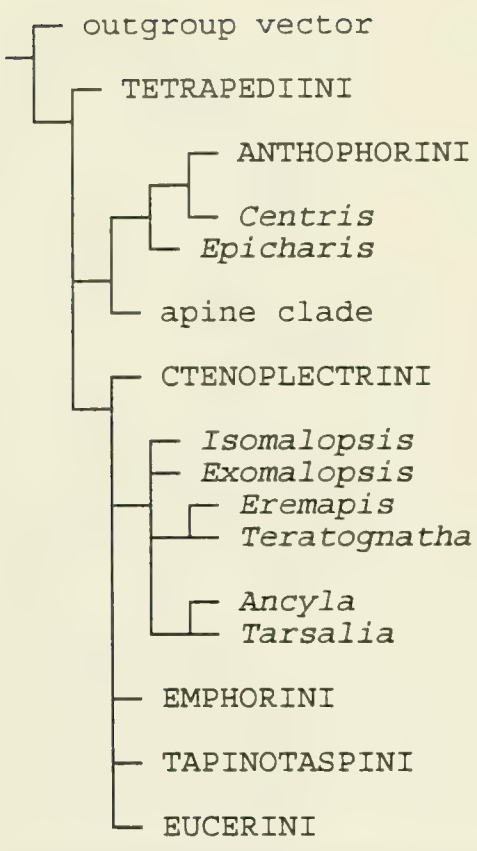
Ancylini: The monophyly of the Ancylini was not unequivocally demonstrated in the analysis, although it was supported in most of the trees obtained. In the 1684 minimum-length trees that resulted from Analysis 1A, there were four different arrangements of *Ancyla* and *Tarsalia* (Fig. 6). They appeared as sister groups in three of these arrangements (exemplified by Figs. 6b,c,d). Among the 138 minimum-length trees from Analysis 2A, there were 11 different arrangements of *Ancyla* and *Tarsalia* (Figs. 7 , 8 and 9). They were sister taxa in nine sets of these arrangements (Figs. 7b,c,d,e,f,g, 8a,b and 9a). They were also sister taxa in all minimum-length trees from analyses 2B and 3B (Figs. 4 and 5).

Only one character supported the monophyly of this tribe in all of these trees: gonocoxite with ventrolateral oblique sulcus, but with no septum (Character 123-1), which is a unique feature among the pollen-collecting apine bees. Different sets of additional characters supported the sister-group relationship of these genera in different topologies.

In those trees where *Ancyla* and *Tarsalia* were not sister groups, they appeared either as the two basal branches of Exomalopsini (Fig. 7a) or with *Ancyla* as the basal branch of the Apinae and Exomalopsini and *Tarsalia* as the next two branches (Fig. 9b).

It is worth pointing out that most apomorphies for *Ancyla* cannot be distinguished from states found in the hypothetical ancestor for all long-tongued bees (as indicated by Roig-Alsina & Michener). These are characters in the mouthparts (Characters 39-52), but also inside the head, and in the thorax, legs and male genitalia. The presence of an elevated polished area in the base of labrum (Character 8-

a



b

	1	**2**	**3**	**4**	**5**	**6**	**8**	**10**	**11**	**12**
	10	0	2	1	10	0	10	1	10	10
	13	**14**	**16**	**17**	**20**	**21**	**22**	**23**	**24**	**27**
	10	1	1	1	0	0	1	0	1	10
	28	**29**	**30**	**32**	**33**	**35**	**36**	**37**	**38**	**39**
	10	10	0	4	10	0	0	3	3	0
	40	**41**	**43**	**44**	**45**	**46**	**47**	**48a**	**48b**	**49**
	10	4	4	0	10	10	0	10	0	2
	50	**51**	**52**	**53**	**54**	**55**	**56**	**58**	**60**	**61**
	1	0	2	10	0	0	10	3	10	10
	62	**63**	**64**	**65**	**66**	**67**	**68**	**69**	**70**	**71**
	1	2	2	10	10	10	3	0	0	0
	72	**73**	**74**	**75**	**76**	**77**	**78**	**79**	**80**	**81**
	2	4	2	6	10	10	3	0	1	0
	82	**83**	**84**	**85**	**86**	**87**	**88**	**89**	**90**	**91**
	1	3	4	4	10	4	3	0	3	1
	92	**93**	**94**	**95**	**96**	**97**	**98**	**99**	**100**	**101**
	0	0	0	0	1	10	0	10	3	1
	102	**103**	**104**	**105**	**106**	**107**	**109**	**110**	**113**	**116**
	0	2	2	0	10	1	10	0	4	10
	118	**119**	**120**	**121**	**122**	**123**	**124**	**125**	**126**	**127**
	1	1	4	2	10	10	3	1	0	2
	128	**130**	**131**							
	3	10	10							

Fig. 5. a. Summary of the consensus tree for the 8 shortest trees (length = 744, ci = 68, ri = 84) obtained in Analysis 3B. Monophyletic groups were collapsed and represented by tribe names. **b.** Weights applied for each character (character numbers in boldface).

0) is unique among all apine bees studied. This large set of plesiomorphic-like apomorphies might suggest wrong phylogenetic placement for *Ancyla*. However, many characters (Figs.7, 8 and 9) support its placement among the long-tongued bees, even in its presumably reduced mouthparts (Silveira, in press).

Relationship between Exomalopsini and Ancylini: The relation between Exomalopsini and Ancylini could not be clearly determined. A sister-group relationship between them is supported by eight of the eleven different positions for *Ancyla* and *Tarsalia* in Analysis 2A, and also by the results of Analysis 2B (Fig. 4). The possibility also exists, as suggested by some of the trees obtained (e.g. Fig. 7a), that *Ancyla* and *Tarsalia* are the two basal branches of Exomalopsini.

The only features to support the sister group relationship between Ancylini and Exomalopsini in Analysis 2B were Characters 58-0 (paraglossa beyond apex of suspensorium less than 1.3 times the length of suspensorium) and 73-0 (propodeal profile with a nearly horizontal basal zone behind which it abruptly turns downward to form the declivous posterior surface). Neither of these features is exclusive to Ancylini and Exomalopsini, however. Character 58-0 is a reversion to the condition in the apine ancestor. It is found as a reversion also in *Diadasina* and *Caenonomada*. It is a plesiomorphy for Tetrapediini, and for the anthophorine and apine clades. Within Exomalopsini, *Teratognatha* presents state 1, which appears also in *Ctenoplectra* and as a synapomorphy for Eucerini + Emphorini + Tapinotaspini. Character 73-0 appears also in *Eucerinoda*.

Relationships among other Apinae: The results suggest that the Apinae may have evolved through two major lines: one (from here on called the apine line) consisting of the Centridini, Anthophorini and the apine clade, and the other (from here on, the eucerine line), of the Eucerini, Emphorini, Tapinotaspini, Ancylini and Exomalopsini (but see results of Analysis D in Roig-Alsina & Michener). The positions of Tetrapediini and Ctenoplectrini, however, are dubious in this scheme.

Tetrapediini was frequently presented as the basal branch of the Apinae. In such cases Ctenoplectrini was always placed in the eucerine line. In other trees, Ctenoplectrini appears as the basal group of the apine line, in which case Tetrapediini is the second branch.

In Analysis 2B, the apine line, which excluded Ctenoplectrini, is supported by Characters 40-0 (stipital sclerite of maxilla distinct) and 104-2 (stigma of forewing small, about

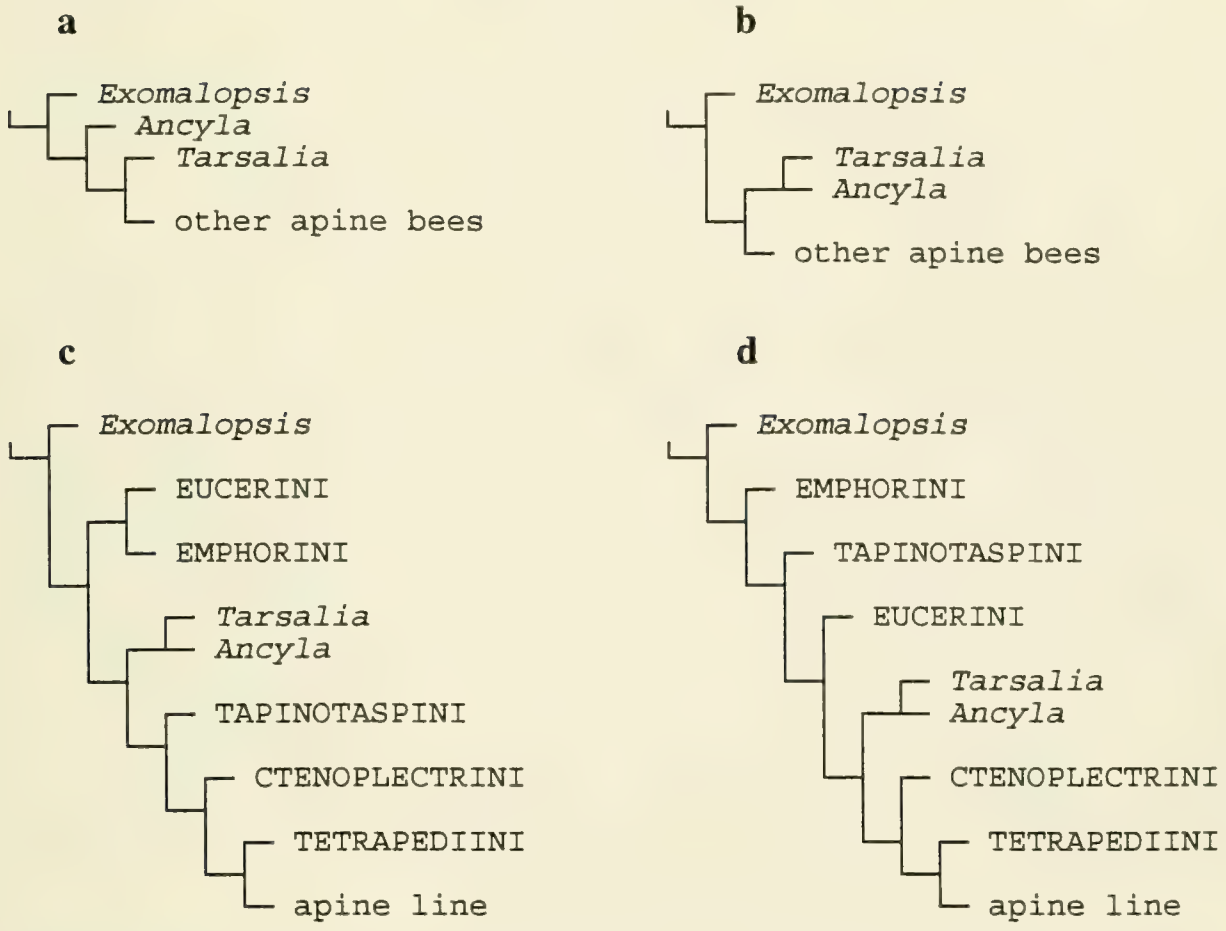


Fig. 6. Positions occupied by *Ancyla* and *Tarsalia* among the Apinae in the 1684 shortest trees found in Analysis 1A.

as long as broad to nearly absent). The latter is variable in the apine line and is also present in the Eucerini, in *Tarsalia* and in some *Exomalopsis*. Other characters support the apine line without Ctenoplectrini in one or other of the different trees.

The relationships among Centridini, Anthophorini and the apine clade were stable throughout the analyses performed here and were the same as those yielded by Roig-Alsina & Michener's analysis "D".

The eucerine line (including Ctenoplectrini) is supported in Analysis 2B by Characters 120-0 (S7 of male with two or four apical lobes) and 14-2 (union of anterior tentorial arm to head wall forming a large triangular subantennal area). These characters were also somewhat variable. Within the eucerine line, *Isomalopsis* and *Monoeca* have 120-1, which is the condition of all bees in the apine line except *Apis* which has 120-2. Character 14 is variable in Exomalopsini and Emphorini and 14-1 is the condition in the Eucerini; 14-2 does not appear in the apine line.

DISCUSSION AND CONCLUSIONS

Roig-Alsina & Michener anticipated that the monophyly of Exomalopsini might be demonstrated if more characters were found in further analyses. They already mentioned that Characters 3 and 75 were suggestive of this hypothesis. The variation of the integument of the specialized region in the paraocular area (Character 3) was characterized by a relatively small consistency index when evaluated as a whole (ci = 23); the state present in the Exomalopsini, however, is found only in this tribe and in *Tapinotaspis*. Character 75 could not be checked for *Ancyla* and *Tarsalia;* if they possess the same feature as the Exomalopsini, the hypotheses that Ancylini and Exomalopsini are sister-groups or that they are part of a single monophyletic group would be strengthened.

A third character pointed out by Roig-Alsina & Michener as supportive of the monophyly of Exomalopsini was the basal constriction of the inner margin of the first segment of labial palpus. This feature, however, is also present in Tapinotaspini and in *Ancyla* and *Tarsalia* and might indeed be a synapomorphy for a clade including the three groups.

Even if a sister-group relationship for *Ancyla* and *Tarsalia* had been supported in all trees in the present analyses, since only one species of each taxon was employed, the possibility still would exist that *Tarsalia* is paraphyletic in rela-

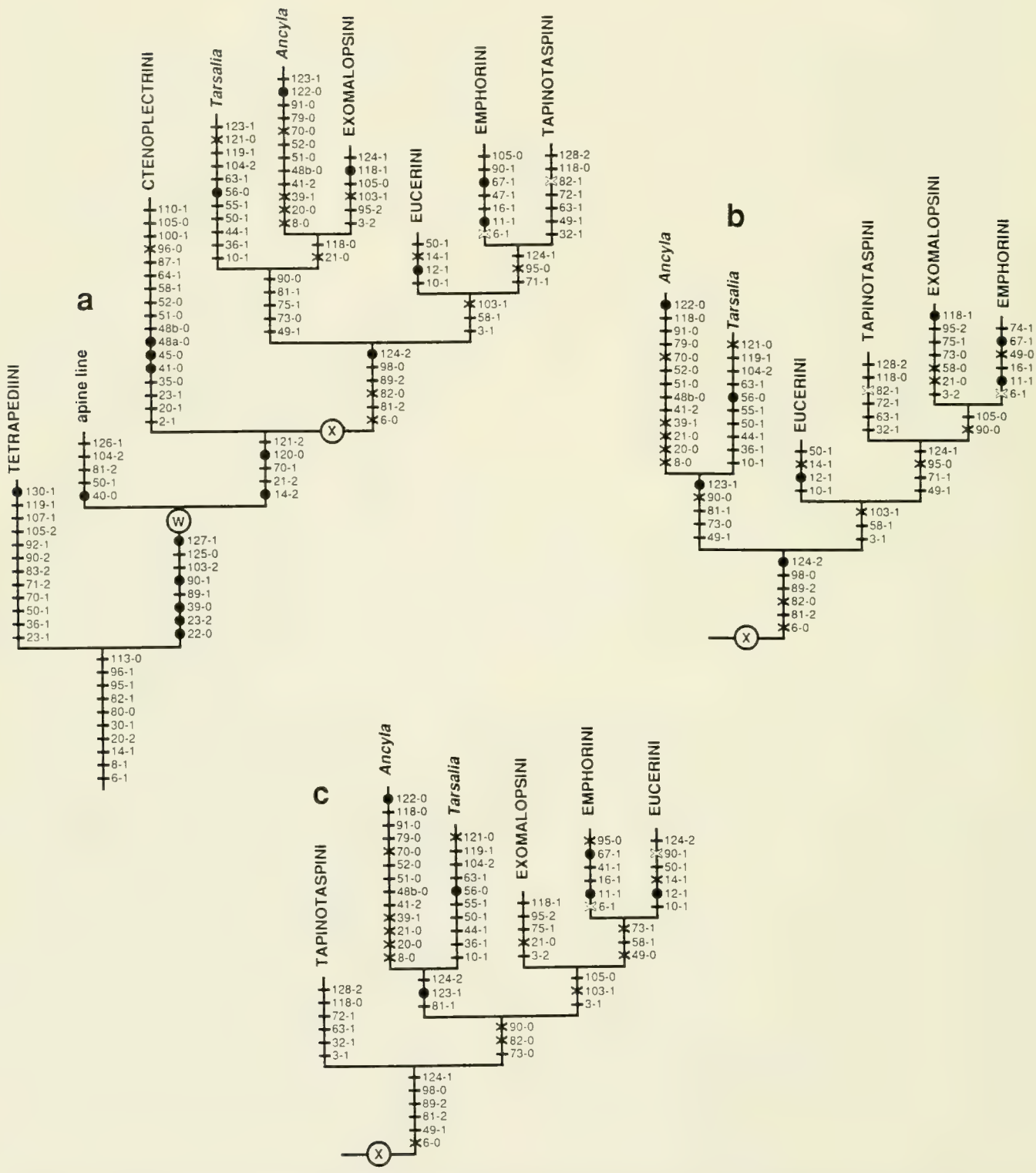
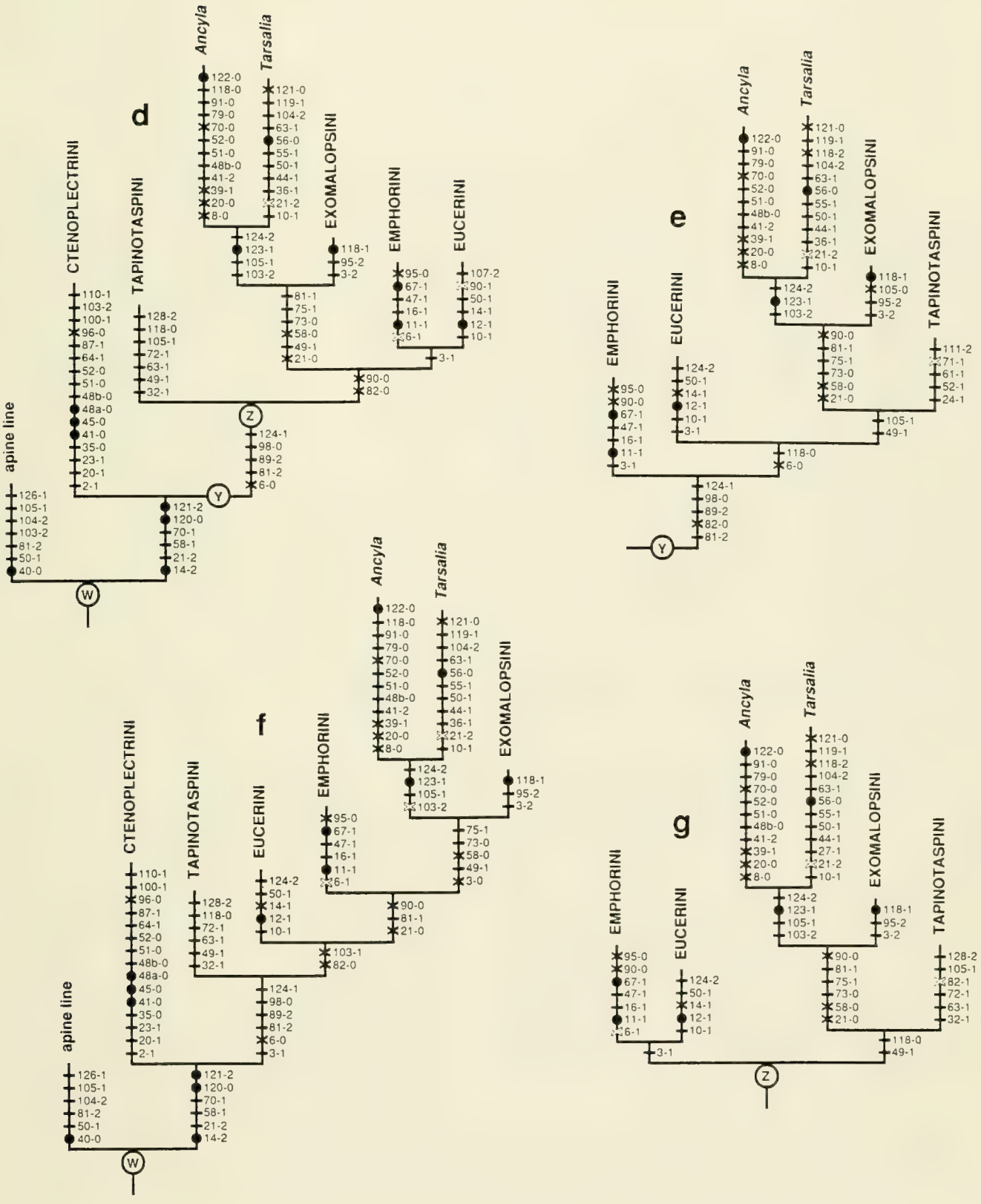


Fig. 7. Positions in which *Ancyla* and *Tarsalia* appeared among the apine bees in the 138 most parsimonious trees obtained in Analysis 2A, topologies in which Tetrapediini is the first branch of Apinae and Ctenoplectrini is the basal branch of the "eucerine line". The basal portions of cladograms beginning in circled-letters (W to Z) are identical to branches below these same letters in other cladograms.

(Continued on page 171)


d
CTENOPLECTRINI
TAPINOTASPINI
Ancyla
Tarsalia
EXOMALOPSINI
EMPHORINI
EUCERINI
apine line
e
f
g
W
Y
Z

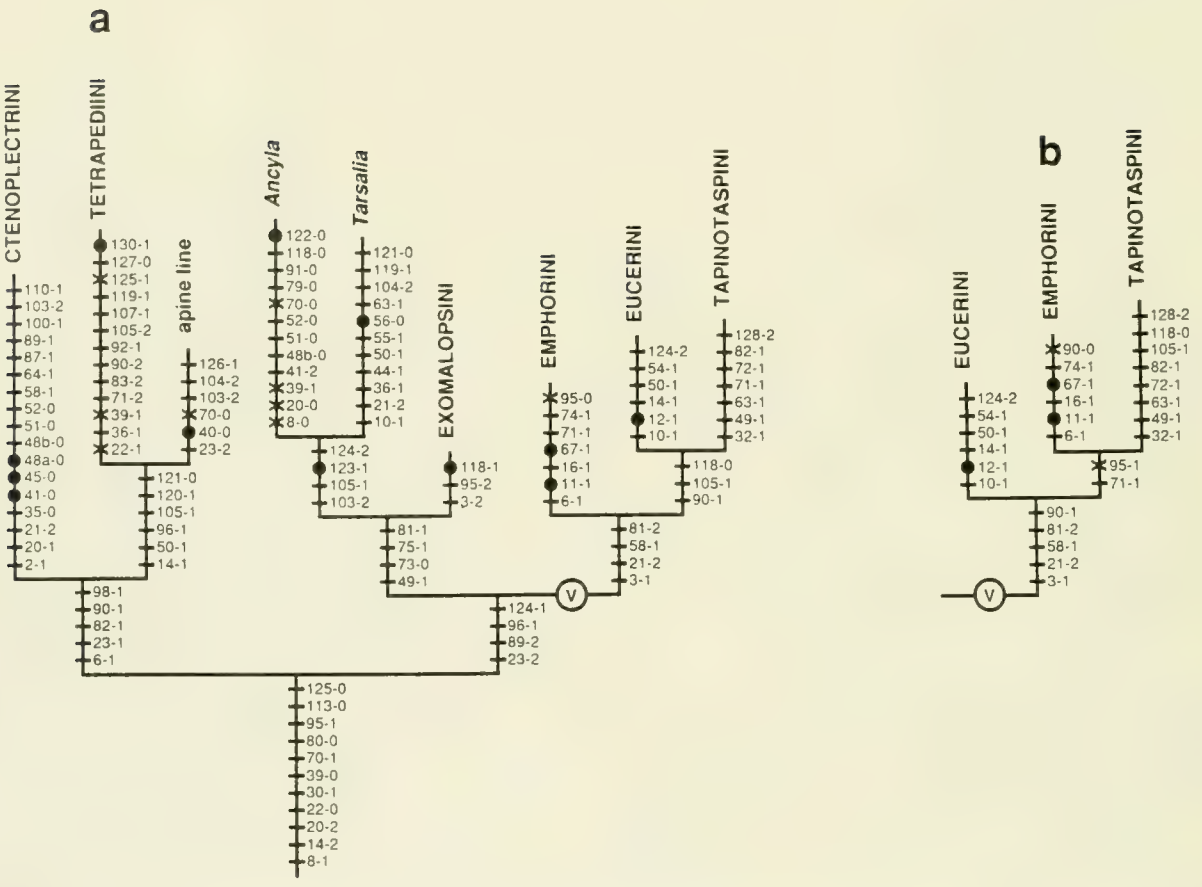


Fig. 8. Positions in which *Ancyla* and *Tarsalia* appeared among the apine bees in the 138 most parsimonious trees obtained in Analysis 2A, topologies in which Ctenoplectrini and Tetrapediini are the first branches of the "apine line". The basal portions of Cladogram b are identical to branches below the circled V in Cladogram a.

tion to *Ancyla*. In this case, Warncke (1977, 1979) might be correct in putting them together in the same genus.

Considering the uncertain sister-group relationship between *Ancyla* and *Tarsalia* and the uncertain close relationship between them and Exomalopsini, it seems advisable to keep the former as separate genera, constituting a tribe separate from the Exomalopsini, until better evidence is brought to light.

New characters have not been presented that strengthen the support for the "apine line", which was already suggested by the analyses made by Roig-Alsina & Michener. However, the fact that it consistently reappears with the same topology in all local parsimony analyses increases one's confidence in its reality, in spite of the few and weak characters that support it, as discussed by Roig-Alsina & Michener.

LITERATURE CITED

Ashmead, W. H. 1899. Classification of the bees or the superfamily Apoidea. Transactions of the American Entomological Society 26: 49-100.

Dalla Torre, C. G. de. 1896. Catalogus Hymenopterorum Hucusque Descriptorum, Systematicus et Synonymicus. Vol 10: Apidae (Anthophila). 643pp. Leipzig: Engelmann.

Dalla Torre, C. G. de & H. Friese. 1895. Synonymischer Katalog der europäischen Sammelbienen. Entomologische Nachrichten 21(3): 37-50.

Farris, J. S. 1969. A successive approximations approach to character weighting. Systematic Zoology 18: 374-385.

Farris, J. S. 1988. Hennig86 Reference. Version 1.5. Port Jefferson Station, New York, distributed by the author.

Lepeletier, A. 1841. Histoire Naturelle des Insects. Hyménoptères. Vol 2. 680p. Paris: Libraire Encyclopédique de Roret.

Maddison, W. P., M. J. Donoghue & D. R. Maddison. 1984. Outgroup analysis and parsimony. Systematic Zoology 33: 83-103.

McGinley, R. J. & J. G. Rozen, Jr. 1987. Nesting biology, immature stages, and phylogenetic placement of the Palaearctic bee *Pararhophites* (Hymenoptera: Apoidea). American Museum Novitates 2903: 1-21.

Michener, C. D. 1944. Comparative external morphology, phylogeny, and a classification of the bees (Hymenoptera). Bulletin of the American Museum of Natural History 82: 156-326.

Michener, C. D. 1979. Biogeography of the bees. Annals of the Missouri Botanical Garden 66: 277-347.

Michener, C. D. & J. S. Moure. 1957. A study of the classification of the more primitive non-parasitic anthophorine bees (Hymenoptera, Apoidea). Bulletin of the American Museum of Natural History 112: 395-452.

Popov, V. V. 1949. The tribe Pararhophitini (Hymenoptera, Anthophorinae) as an early Tertiary element of the recent desert fauna of Central Asia and Egypt. Doklady Akademii Nauk SSSR 66: 507-510. [In Russian].

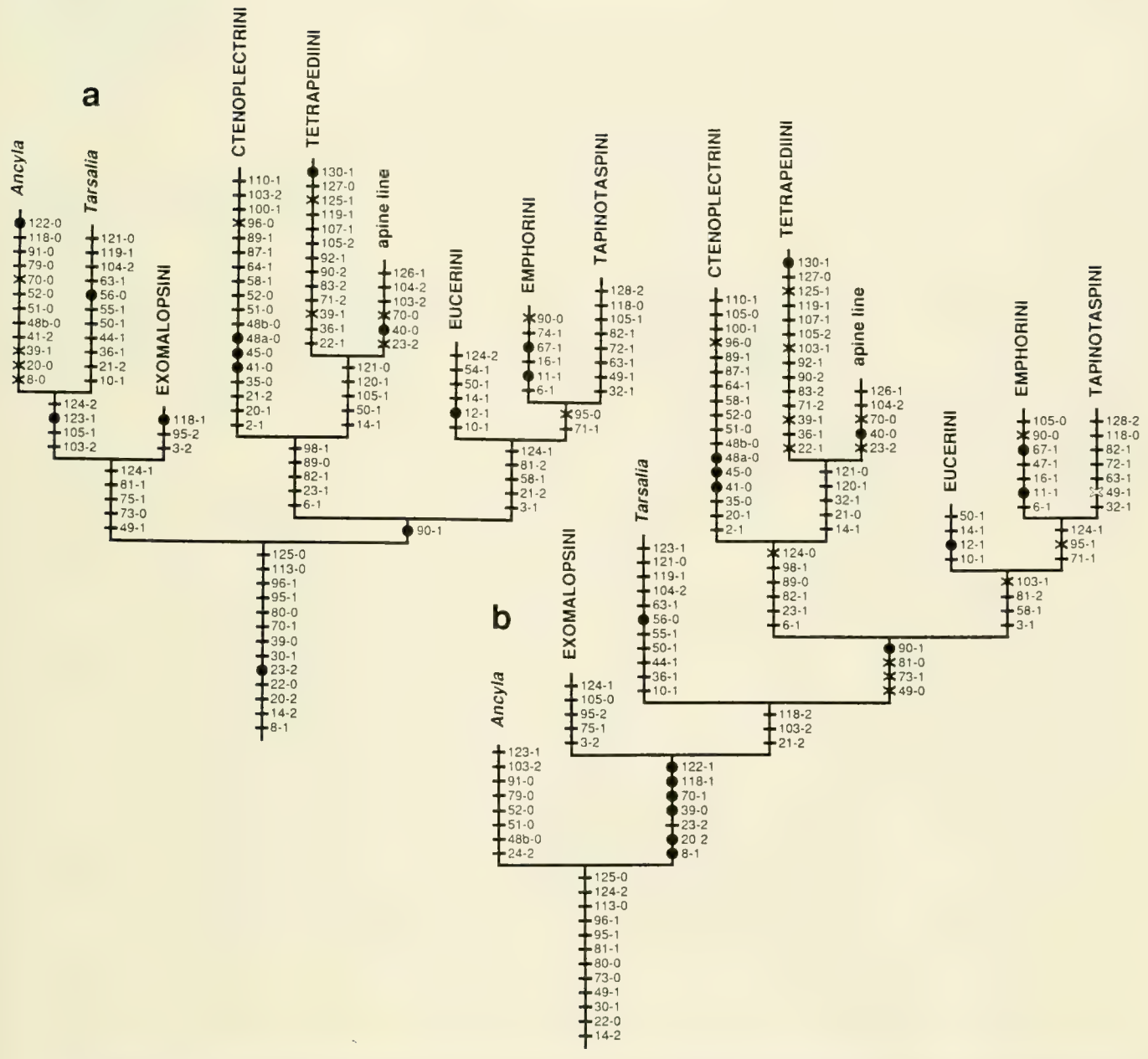


Fig. 9. Positions in which *Ancyla* and *Tarsalia* appeared among the apine bees in the 138 most parsimonious trees obtained in Analysis 2A, topologies in which Ctenoplectrini and Tetrapediini are the first branches of the "apine line".

Roig-Alsina, A. & C. D. Michener. 1993. Studies of the phylogeny and classification of long-tongued bees (Hymenoptera: Apoidea). University of Kansas Science Bulletin 55: 124-162.

Silveira, F. A. (in press). The mouthparts of *Ancyla* and the reduction of the labiomaxillary complex among long-tongued bees (Hymenoptera: Apoidea). Entomologica Scandinavica.

Toro, H. 1976. *Chilimalopsis*, nuevo genero Chileno de Exomalopsini (Hymenoptera: Apoidea). Anales del Museo de Historia Natural de Valparaiso 9: 73-76.

Warncke, K. 1977. Ideen zum natürlichen System der Bienen (Hymenoptera, Apoidea). Mitteilung Münchener Entomologischen Gesellschaft 67: 39-63.

Warncke, K. 1979. Beiträge zur Bienenfauna des Iran: 10. Die Gattung *Ancyla* Lep., mit einer Revision der Bienengattung *Ancyla* Lep. Bollettin del Museo Civico di Storia Naturale di Venezia 30: 183-195.

ANNOUNCEMENT

The *University of Kansas Science Bulletin* (continuation of the *Kansas University Quarterly*) is an outlet for scholarly scientific investigations carried out at the University of Kansas or by University faculty and students. Since its inception, volumes of the *Bulletin* have been variously issued as single bound volumes, as two or three multi-paper parts or as series of individual papers. Issuance is at irregular intervals, with each volume prior to volume 50 approximately 1000 pages in length. Effective with volume 50, page size has been enlarged, reducing the length of each volume to about 750 pages.

The supply of all volumes of the *Kansas University Quarterly* is now exhausted. However, most volumes of the University of Kansas Science Bulletin are still available and are offered, in exchange for similar publications, to learned societies, colleges and universities and other institutions, or may be purchased at $30.00 per volume. Where some of these volumes were issued in parts, individual parts are priced at the rate of 3 cents per page. Current policy, initiated with volume 46, is to issue individual papers as published. Such separata may be purchased individually at the rate of 7 cents per page, with a minimum charge of $1.50 per separate. Subscriptions for forthcoming volumes may be entered at the rate of $30.00 per voluem. All communications regarding exchanges, sales and subscriptions should be addressed to the Exchange Librarian, University of Kansas Libraries, Lawrence, Kansas 66045.

Individual papers for personal use by investigators are available for most recent and many older issues of the Bulletin. Such requests should be directed to the author or to the relevant Museum or Department of the University of Kansas.

The International Standard Serial Number of this publication is US ISSN 0022-8850.

Editor
Charles D. Michener

Editorial Board
Meredith Lane, *Chairman*
James S. Ashe
George W. Byers
Christopher Haufler
Norman A. Slade

MCZ LIBRARY MAY 19 1994 HARVARD UNIVERSITY

THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. 55, No. 6, pp. 175-238 March 30, 1994

Species-Groups and Cladistic Analysis of the Cleptoparastic Bee Genus *Nomada* (Hymenoptera: Apoidea)[1]

Byron A. Alexander[2]

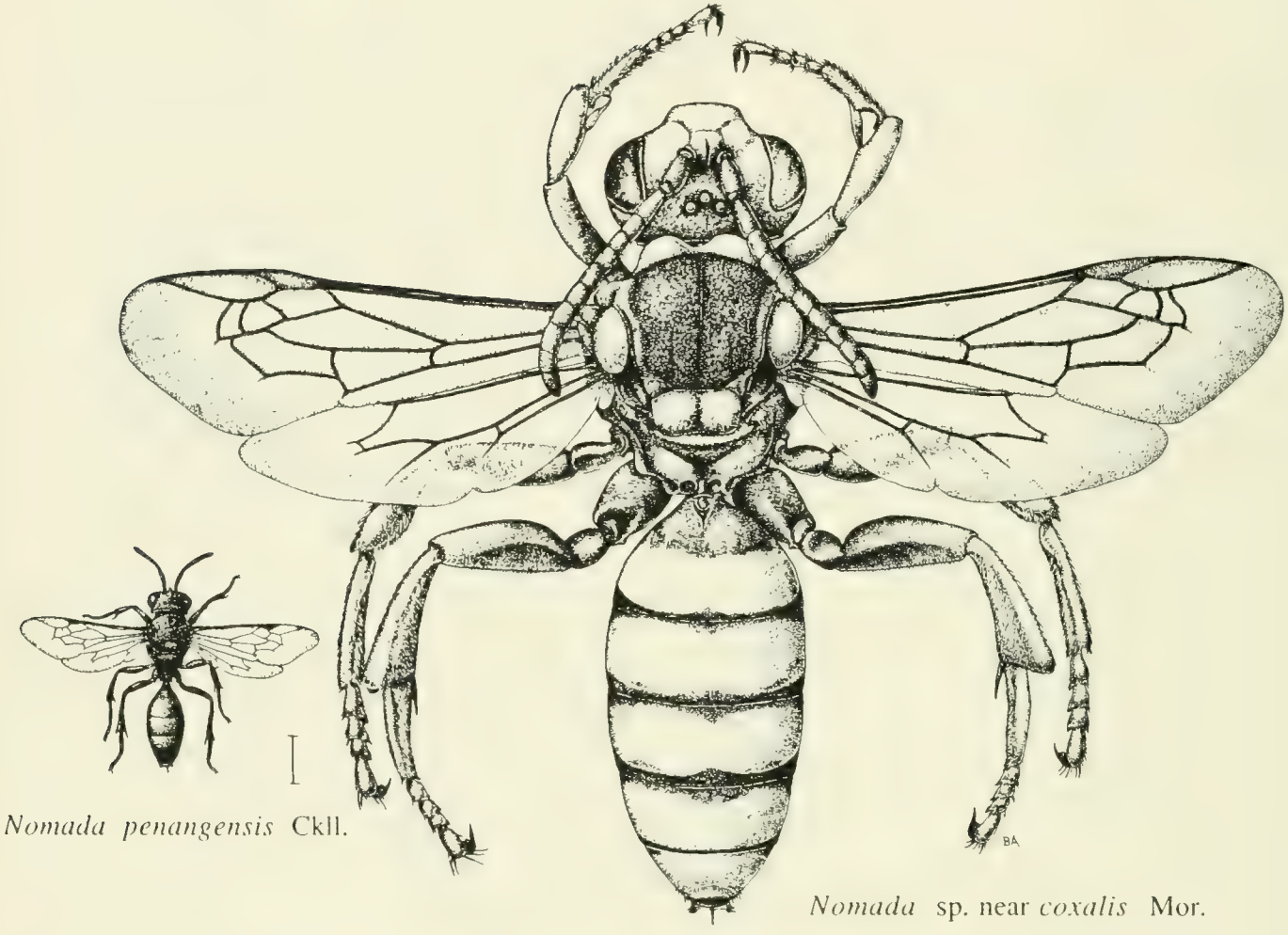
TABLE OF CONTENTS

Abstract 175
Introduction 177
Materials and Methods 177
Previous Taxonomic Treatments of *Nomada* 178
The Monophyly of *Nomada* 178
Cladistic Analysis 179
Analysis 1. Hypothetical Ancestor as an Outgroup 182
Analysis 2. Ten Nomadine Taxa as an Outgroup 190
The Question of Subgeneric Classification of *Nomada* 193
Characters Employed in Descriptions of Species Groups 195
Descriptions of Species Groups 207
Genus *Nomada* Scopoli p. 207, *gigas* group p. 207, *integra* group p. 212, *adducta* group p. 214, *vincta* group p. 215, *odontophora* group p. 216, *vegana* group p. 217, *roberjeotiana* group p. 218, *erigeronis* group p. 220, *rodecki* p. 221, *ruficornis* group p. 222, *armata* group p. 224, *belfragei* group p. 225, *superba* group p. 225, *basalis* group p. 226, *bifasciata* group p. 228, *trispinosa* group p. 229, *furva* group p. 230
Discussion 231
Acknowledgments 233
Literature Cited 234
Appendix: Outgroup Taxa Examined 236

ABSTRACT

The nearly cosmopolitan genus *Nomada* Scopoli is examined on a worldwide basis. A monophyletic *Nomada* that corresponds closely to the genus as it has been understood by most authors can be defined on the basis of apomorphic characters of the terminal metasomal segments of females and certain aspects of the male genitalia and associated sterna. Clear and unequivocal monophyletic groupings within *Nomada* are difficult to identify, and cladistic analyses do not discover a single most parsimonious cladogram for the groupings that are identified. A formal cladistic classification recognizing subgenera is considered premature, in view of the difficulty of defining monophyletic groups and resolving phylogenetic relationships among them. Nevertheless, an informal classification into species groups is proposed. Descriptions and diagnoses of the groups are presented, and information on geographic distribution and host relationships is briefly summarized in the species group descriptions.

[1] Contribution number 3128 from the Department of Entomology, University of Kansas, Lawrence.
[2] Department of Entomology and Snow Entomological Museum, Snow Hall, University of Kansas, Lawrence, Kansas 66045-2119, USA.



Frontispiece. Size variation within the genus *Nomada*. The small individual is an adult female of *Nomada penangensis* Cockerell, and the large bee is an adult female of an undescribed species close to *Nomada coxalis* Morawitz. Scale indicates 1 mm.

INTRODUCTION

Most lineages of cleptoparasitic bees have produced only a few species, while a few have become very speciose. One of the most striking examples of the latter pattern is the genus *Nomada*. This genus is placed in the subfamily Nomadinae, a large assemblage of cleptoparasitic long-tongued bees containing some 33 genera and over 1,200 species (Roig-Alsina, 1991). Although the total number of species in *Nomada* is unknown, it appears that this one genus contains well over half of the species in the Nomadinae.

Species of *Nomada* occur on all the continents (except Antarctica), although most are in the northern hemisphere. The species-level taxonomy is still very poorly known over major portions of the range of the genus. This is especially true in western North America, where only a few small groups have been recently revised at the species level (Evans, 1972; Broemeling, 1988; Broemeling & Moalif, 1988), in most of Asia, where the genus is undoubtedly common but poorly studied, and in Central and South America, where there are far fewer species described than in North America. In his general species-level revision of all bees of the eastern United States, Mitchell (1962) included keys and descriptions for *Nomada*, but his knowledge of the genus was rather superficial. The species of *Nomada* are best known for the western Palearctic, where Maximilian Schwarz has been studying them for the past thirty years, and for Japan, where Katsuji Tsuneki has published recent comprehensive revisions. Eardley and Schwarz (1991) have recently revised the *Nomada* of sub-Saharan Africa, where only 10 species occur. About 45 species have been described from the Oriental region, seven from New Guinea and nearby islands (Timor, Seram, Bismark Archipelago, Solomon Islands), and one from northeastern Australia. The only recent treatment of *Nomada* from tropical Asia is that of Schwarz (1990), who dealt with most of the species that have been described from India, Sri Lanka, Pakistan, and Burma.

There have been no prior attempts to provide a comprehensive review of the entire genus *Nomada*. Although the picture to be presented here is preliminary and incomplete, the potential value of a broad overview of *Nomada* is that it can provide a more evolutionarily meaningful frame of reference for future work than studies based on arbitrary geographic boundaries. The major goals of this paper are to provide an explicit definition of the genus *Nomada* as a monophyletic lineage (sensu Hennig, 1966), to identify major monophyletic subgroups within the genus, and to present a preliminary hypothesis of the cladistic relationships among these subgroups.

MATERIALS AND METHODS

I have studied specimens of over 800 described and undescribed species of *Nomada* from the entire extent of its geographic range. For material from the Old World, especially from the western Palearctic region, I have relied extensively on material determined by M. Schwarz, both from his personal collection, where I was able to examine 318 described and undescribed species and subspecies, and in the collections of the American Museum of Natural History (AMNH), the Natural History Museum (in London, BMNH), Cornell University (CUIC), and the U.S. National Museum of Natural History (USNM). The BMNH was an important source of primary type specimens from Asia, sub-Saharan Africa, and Australia. Several other institutions, listed in the Acknowledgements, also generously provided specimens from the Old World for me to examine.

For Japanese *Nomada*, I have been able to examine material determined by K.Tsuneki, because the Tsuneki collection has recently been acquired by the USNM. Tsuneki (1973, 1975, 1976a, 1976b, 1986) has so far recognized 82 species and subspecies of *Nomada* from Japan. Twenty eight of these taxa (34%) have been described from only a single specimen, and an additional 12 taxa are based on no more than 4 specimens each. Because Tsuneki's primary types are not in the USNM collection (with two exceptions), I have not seen representatives of most of the Japanese species that are known only from holotypes. The Japanese *Nomada* in the USNM collection represent 37 species determined by Tsuneki. However, his published species descriptions are very thorough and include explicit comparisons with other species, so it has usually been possible to determine the species-groups of the Japanese species names for which I have not personally examined accurately determined specimens.

Because the species-level taxonomy is so poorly known for North American *Nomada*, I have relied heavily on examination of primary type specimens from this geographic region. Altogether, I have examined holotypes or lectotypes of 276 of the 314 species (87%) of North American *Nomada* listed in the most recently published catalog (Hurd, 1979). Of the 38 taxa for which I have not seen types, 4 are taxa for which the original types have been lost or destroyed, and I have seen paratypes or, in one case, a homotype for an additional 9 taxa. There are several taxa for which I have seen determined specimens, but not authentic type material, so that the identity of these specimens remains in some doubt. There are only 8 described species of North American *Nomada* for which I have seen no specimens at all.

The majority of specimens of North American *Nomada* are currently on loan to the Natural History Museum of Los Angeles County, where R.R. Snelling is studying them. During an extended visit to this museum, I had the opportunity to examine material that R.R. Snelling, P.H. Timberlake, and G.E. Bohart had identified as representing no fewer than 110 still undescribed North American species of *Nomada*, primarily from the western portions of the continent.

There are 35 names for Neotropical species of *Nomada* listed in Snelling's recent (1986) revision. I have examined holotypes or lectotypes for 17 of these taxa, as well as specimens of another 5 species that I consider to be accurately determined (courtesy of A. Roig-Alsina of the Museo Argentino de Ciencias Naturales in Argentina). I have also examined undetermined South American material that contains at least 5 species not corresponding to any accurately determined species I have seen. Because every Neotropical specimen of *Nomada* that I have examined clearly belongs in a single, well-defined monophyletic group (the genus *Hypochrotaenia* as defined by Snelling, or the *vegana* species-group as defined herein), I have not considered it necessary for the purpose of this study to locate and examine every type specimen from the Neotropical region.

More detailed information on which species I have examined is included in the Descriptions of Species Groups, and all species names, including those that cannot be assigned to species groups, are listed in Alexander and Schwarz (1994).

Male genitalia and the female sting apparatus were dissected from relaxed specimens and cleared overnight at room temperature in 10% KOH, then transferred to dilute acetic acid followed by distilled water. The dissected parts are stored in glycerin in genitalia vials on the same pins as the specimens from which they were dissected.

Drawings were done in pencil with a drawing tube (a few freehand drawings were also made during visits to research collections), and subsequenty rendered in ink. Scanning electron micrographs were taken by E. R. Hoebeke of the Department of Entomology of Cornell University, using the University's SEM facility. The methods used in the cladistic analysis will be described in detail in a later section.

PREVIOUS TAXONOMIC TREATMENTS OF *NOMADA*

Occasional attempts have been made to partition *Nomada* into smaller genera. By far the most ambitious was that of Robertson (1903) in North America. Declaring that "there has been enough confusion in this group to suit the most stupid of lumpers", he split North American *Nomada* into nine genera, six of which were described as new. He accomplished all this in only eight pages of text, which included keys to all of the 32 species known to him. His generic descriptions are in the form of rather brief couplets in his key to genera (on p. 173, he explicitly elevated *Micronomada* to generic rank, but it is not included in his key to genera). Neither his contemporaries nor subsequent workers accepted his decisions about generic rank, although the new names he proposed have been widely used as subgenera. North American workers in general, starting with Cockerell and Atkins (1902), have used the subgenus concept. In a revision of the species of Nebraska and adjacent states, Swenk (1913, 1915) discussed the subgenera recognized at that time in considerable detail, acknowledging that "the group as a whole seems to intergrade at various points in practically every promising character which has been employed and tested", but arguing that "various fairly well defined though intergrading groups are recognizable". Swenk proposed no new subgenera himself, but Rodeck (1945, 1947) later described three, and Snelling (1986) and Broemeling (1988) have recently added three more, although Snelling (1986) also synonymized seven previously recognized subgenera.

Almost all Old World workers have preferred not to recognize subgenera, referring instead to species groups, usually in a vague and informal manner. The only explicit list providing names of these groups and their included species for the entire genus (in Europe) is in Schmiedeknecht (1882). He clearly stated that the groupings were provisional and based primarily upon color patterns, and were simply for convenience in identification. Perkins (1919, pp. 315-316) placed the British species into groups, which he did not name even informally. He only mentioned defining characters for one group. Schwarz (1967) revised the *cinctiventris* group (which is restricted to the western Palearctic) and presented defining characters for the group as well as a list of included species. The primary focus of his research has been identifying and describing species. He has routinely referred to species groups in his publications, but he usually has not defined them or provided lists of included species (except for the *fuscicornis* group [Schwarz, 1974, 1977] and the previously mentioned *cinctiventris* group). E. Stöckhert (1942, 1943) also published careful, detailed revisions of two species groups in central Europe, the *zonata* group and the *furva* group. His revisions contain keys and excellent descriptions of the included species, but are limited in geographic perspective. He was also rather vague about the diagnostic characters for his species groups, although he was very explicit about diagnostic characters for the included species. Tsuneki (1973, 1975, 1976a, 1976b, 1986) has published detailed descriptions of the *Nomada* of Japan, but his discussions of their relationships to species from other regions are limited to statements about where they would run in Schmiedeknecht's (1882) or Pittioni's (1952) keys to European species.

Warncke (1982) recognized two subgenera of *Nomada* in the Old World: *Acanthonomada* (originally described as a genus by Schwarz in 1966) and *Nomada*. In 1986, independently of Snelling (1986), Schwarz proposed that *Nomadita* Mocsáry (1894) be assigned subgeneric rank within *Nomada* and noted that it is a senior synonym of Rodeck's (1945) New World subgenus *Callinomada*. Schwarz listed the western Palearctic species included in the subgenus and identified synonyms for these species.

To date, the most comprehensive attempt to explicitly define groupings within *Nomada* has been Snelling's (1986) survey of the New World subgenera. In this work, he partitioned New World *Nomada* into three genera, *Hypochrotaenia*, *Centrias*, and *Nomada*, and he recognized three subgenera for *Hypochrotaenia* and six for *Nomada*. Several previously recognized subgenera were placed in synonymy, and two new subgenera were recognized. Snelling's descriptions and discussions of characters provide a far more explicit characterization of groupings within New World *Nomada* (in the broad sense) than had previously existed, so his revision has provided a valuable contribution to our understanding of the genus. However, he does not provide any phylogenetic analysis of the groups he recognizes. Snelling's remarks about character analysis are brief and are summarized in the following statement (Snelling, 1986, p. 3): "Unless a number of features, and usually not those utilized in species level taxonomy, can be correlated, I am not inclined to accord ... groups [defined by these features] any formal status". The cladistic analysis presented below will present evidence that the two groups that Snelling elevated to generic rank, *Centrias* and *Hypochrotaenia*, are monophyletic, but that naming them as genera makes his genus *Nomada* paraphyletic.

THE MONOPHYLY OF *NOMADA*

One can define a monophyletic genus *Nomada* that closely matches the concept of the genus as it has generally been understood by most bee systematists over the past century. In females, both the fifth and sixth metasomal sterna (hereafter abbreviated as S5 and S6) are specially modified. The apical margin of S5 is broadly emarginate, and each of the shallow lobes that flank the median emargination bears a tuft of stout, bristlelike setae (Figure 1). S6 is mostly internal, the apical margin is truncate or very shallowly emarginate, and the disc of the sternum is subrectangular, with widely separated tufts of short, stout, heavily melanized, clawlike setae on the apicolateral corners (Figure 2). Both of these features are remarkably uniform within *Nomada*, and readily distinguishable from the homologous characters in other nomadine genera. There is one North American species, *Nomada obscurella* (Figure 3), in which S6 is not parallel-sided but instead tapers to the apex, thus superficially resembling the form of S6 in the *Brachynomada* group of genera (sensu Roig-Alsina, 1991 = Brachynomadini of Roig-Alsina & Michener, 1993; Figure 4). However, Roig-Alsina has identified differences in the chaetotaxy and form of the sternal apex that readily distinguish S6 in *Nomada* from other Nomadinae.

I regard the above characters as strong evidence for the monophyly of *Nomada* because they are both distinctive and consistently present within *Nomada*, but they are not present in the outgroup. Another very consistent, but less complex, character of adult females is a pair of tufts of stout, bristlelike setae on metasomal tergum 6 (hereafter abbreviated as T6), one on each side of the pygidial plate (Figure 5). Finally, the apical margin of T5 bears a median area of specially modified setae variously referred to as the prepygidial fimbria or the pseudopygidium. This character is variable within *Nomada*, although none of the alternate states appears

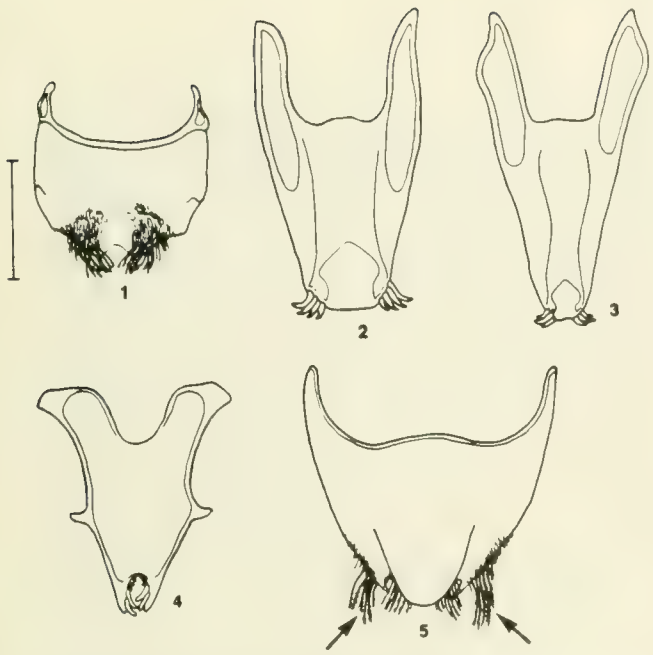


Fig. 1. The characteristic form of female S5 in *Nomada*. The species illustrated is *Nomada articulata* (*erigeronis* group). Scale line indicates 1 mm. **Fig. 2.** Female S6 of *Nomada banksi* (this is the form characteristic of almost all species of *Nomada*). **Fig. 3.** Female S6 of *Nomada obscurella*, the only known species of *Nomada* in which the disc of the sternum tapers to a narrow apex. **Fig. 4.** Female S6 of *Melanomada grindeliae*. Note that in *Melanomada* the apical margin is deeply indented, whereas in *Nomada obscurella* the apical margin is truncate, as in other *Nomada*. **Fig. 5.** Female T6 of *Nomada banksi* (*ruficornis* group). The arrows indicate the tufts of bristlelike setae that are diagnostic of *Nomada*.

to be present in other genera. The most common state in *Nomada* (Figure 6) is for the setae to be broad, flattened, and highly reflective, so that they generally have a white or silvery appearance. The most noteworthy deviations from this state are in the North American species *depressa* and its close relatives, the South African species *N. whiteheadi*, and *Acanthonomada* (equivalent to the *odontophora* species group as defined herein). More detailed study of these setae at higher magnification might reveal additional variation.

Apomorphic features of male morphology tend to vary along the lines of the female pseudopygidium. That is, a variety of alternate derived states can be identified, but there is no derived character as consistent as S5 and S6 of females. The closest thing to such a character for males is the existence of at least a few stout, apically pointed, spinose setae on the median apical process of the eighth metasomal sternum. In some groups, especially the *erigeronis* and *roberjeotiana* species-groups (equivalent to the genera/subgenera *Centrias* and *Nomadita*), these setae are extremely robust and clawlike, and in a few species they are greatly reduced or absent. Because the absence or reduced size of these setae is associated with a variety of other character states that are clearly apomorphic, it is most parsimonious to conclude that the reduction or loss of these setae is derived in these species. Another apomorphic male character that is almost universally present in *Nomada* is an area of modified setae called the subgenital brush on S6. The form of the brush is quite variable (Figure 7) and is useful in defining subgroups within *Nomada*, but in males of other genera in the Nomadinae, I have found nothing resembling any of the states in *Nomada*. However, the subgenital brush is absent in the South African species *Nomada gigas*, and my cladistic analyses indicate that this may be a case of primitive absence rather than secondary loss. Females of *gigas* possess all the defining autapomorphies of *Nomada*.

CLADISTIC ANALYSIS

Although the monophyly of *Nomada* as defined in this study is strongly supported by the characters of adult external morphology discussed in the previous section, several interrelated factors have made cladistic analysis of subgroups within *Nomada* difficult. The first of these is that the phylogenetic position of *Nomada* within the Nomadinae is not entirely clear. This places constraints on the use of outgroup comparison for polarizing characters, because uncertainty about phylogenetic relationships in the outgroup may result in uncertainty about character polarization whenever more than one character state occurs in the outgroup (Maddison et al., 1984). Two different procedures for dealing with this problem will be discussed below.

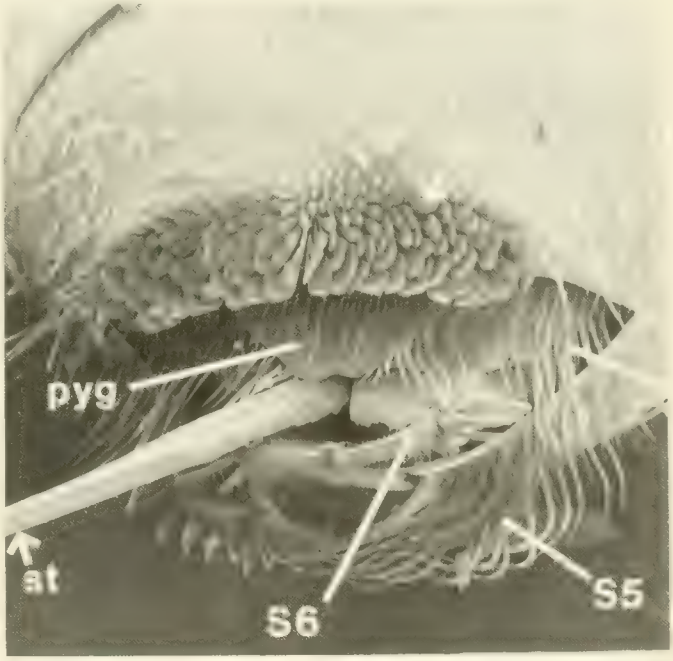


Fig. 6. Apex of metasoma of female *Nomada imbricata* (*ruficornis* group), illustrating the modified terminal metasomal segments characteristic of the genus *Nomada* as they appear in an intact, undissected specimen. **ps** = pseudopygidium or prepygidial fimbria; **pyg** = pygidial plate; **lst** = lateral setal tuft of T6 (cf. Fig. 3); **st** = sting.

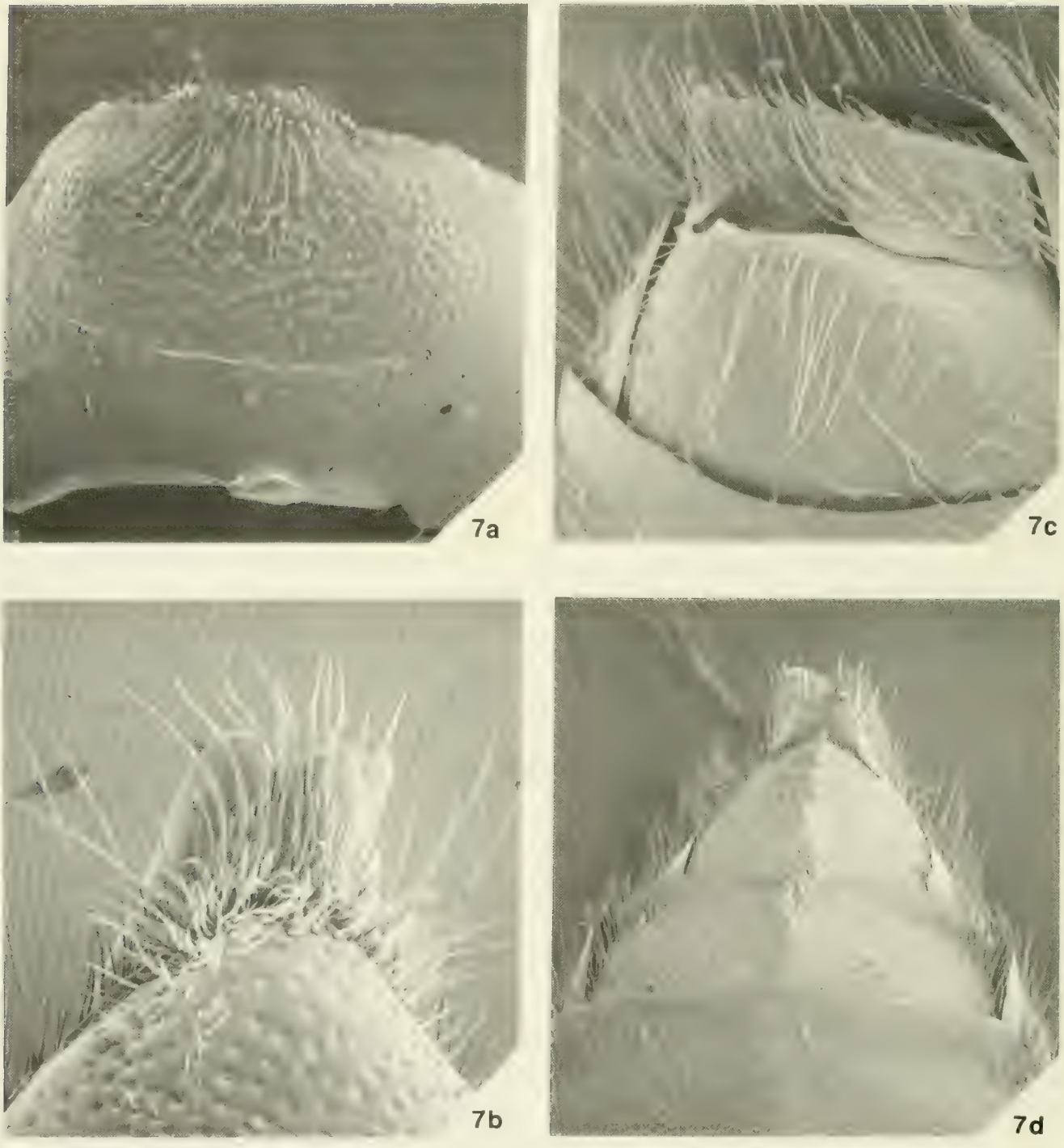


Fig. 7. Subgenital brush on male S6: (a) *Nomada placida* (*roberjeotiana* group), 117x; (b) *N. banksi* (*ruficornis* group), 159x; (c) *N. pilipes* (*vegana* group), 197x; (d) *N. tiftonensis* (*vegana* group), 83 x (*N. pilipes* and *N. tiftonensis* represent the range of variation in the subgenital brush within the *vegana* group.) The specimen of *N. pilipes* illustrated here is somewhat abnormal, in that the setae of the subgenital brush have been bent over in preparation. Ordinarily they would be more or less erect, as in *N.*

tiftonensis.); (e) *N. crotchii* (*erigeronis* group), 58x; (f) *N. articulata* (*erigeronis* group) (*N. crotchii* and *N. articulata* represent the range of variation in the subgenital brush within the *erigeronis* group.); (g) *N. furvoides* (*furva* group), 130x; (h) *N. bifasciata* (*bifasciata* group), 68x.

Another problem has been identifying characters that vary in a manner that is useful for phylogenetic analysis. The most informative characters are those for which discrete alternate states can be identified within the group under study, and one (preferably only one) of these states can be identified in the outgroup. Such characters can be used to identify hypothetical monophyletic groups and to elucidate the phylogenetic relationships among such groups.

Obviously related to the problem of identifying such characters is the problem of identifying monophyletic groups. In the absence of an appropriate character analysis, it cannot be assumed that the groupings (subgenera or species groups) recognized in the existing classification of *Nomada* are monophyletic. The cladistic analyses to be presented below began with an attempt to define homologous characters and alternative states of these characters, and to study the distribution of synapomorphies among the groups that previous *Nomada* workers have proposed. An initial detailed comparative morphological study was made with 43 exemplar species selected to represent the most disparate groups recognized within *Nomada*. For the New World, I used species from each of the subgenera recognized by Snelling; for the Old World, I used specimens provided by Schwarz to represent the range of variation in Old World *Nomada*. Having identified a set of characters to study, I examined all the species of *Nomada*, described and undescribed, that I could locate, as described in the section on methods and materials. Upon completion of my tabulation of character states in all the species I had examined, I proposed the groupings that are used in the cladistic analyses presented below.

The results of these analyses indicated that several of my terminal taxa were paraphyletic. Most of these were incorporated into larger groupings that were monophyletic, although two large paraphyletic assemblages were retained. Thus, the final set of species groups that I am recognizing and formally describing is not identical to the set of groups used as terminal taxa in the cladistic analyses.

A final problem for my cladistic analysis is independence of characters. The rationale for performing a parsimony analysis that identifies the shortest possible tree(s) for a data set is based upon the assumption that each character represents an *independent* hypothesis of homology (and therefore phylogenetic relationships). Although I have carefully examined and tried to use characters from both sexes and from as many different parts of the body as possible, the nature of morphological variation is such that a majority of potentially informative characters are found in males, and especially in the male genitalia. Similar asymmetries in the distribution of cladistically useful characters between sexes have been characteristic of published cladistic analyses of some other groups of bees, such as *Lasioglossum* (McGinley, 1986) and the tribe Anthophorini (Brooks, 1988).

ANALYSIS 1: HYPOTHETICAL ANCESTOR AS AN OUTGROUP.

Method of Assigning Groundplan States to a Hypothetical Ancestor. Maddison et al. (1984) present a detailed and rigorous discussion of outgroup analysis. When one has a fully resolved cladogram that depicts the position of the ingroup and its close relatives, it is a fairly straightforward matter to optimize character state distributions on this cladogram in order to hypothesize which character state was present in the ancestor of the ingroup. Depending on how a given character is distributed in the outgroup, it may or may not be possible to reach a decisive conclusion about the plesiomorphic state of that character in the ingroup, but the method for reaching this decision is clear and unambiguous, and its logical support rests upon the same arguments that justify the use of parsimony methods in cladistics.

Selection of a Cladogram for the Outgroup. Several cladistic analyses have presented hypotheses about the phylogenetic position of *Nomada*. Rozen (1966, 1977; Rozen et al. 1978) has published a series of analyses based on characters of final instar larvae, and Alexander (1990) published an analysis that combined Rozen's larval characters with adult characters taken from the literature. All these studies were based on the hypothesis that the Nomadinae (sensu Michener, 1974; equivalent to the Nomadidae of Linsley & Michener, 1939) is monophyletic. Rozen et al. (1978) presented the most detailed argument supporting the monophyly of this assemblage, citing evidence from larval morphology and the oviposition behavior of adults. However, Roig-Alsina (1989, 1990, 1991) has re-examined adult morphological characters, and he has concluded that Nomadinae in the traditional sense is a polyphyletic assemblage. More precisely, he has proposed that the tribes Isepeolini, Protepeolini, and Osirini, and the genus *Coelioxoides*, should be removed from Nomadinae. At the same time, Rozen (1991) re-evaluated nomadine phylogeny in the light of comparative studies of first instar larvae. (This is the life stage during which the cleptoparasite larva destroys its host, and first instar larvae of these bees are the least like those of other bees.) Although Rozen's 1991 paper does not have any formal cladistic analysis, he supports Roig-Alsina's conclusion that the Nomadinae in the broad sense is not monophyletic. A recent parsimony analysis of exemplars of 82 genera and 38 tribes of long-tongued bees, using both adult and larval morphological characters (Roig-Alsina and Michener, 1993), similarly concluded that *Coelioxoides*, Isepeolini, Protepeolini, and Osirini should be excluded from Nomadinae if the latter is to be monophyletic. Because the earlier cladistic analyses by Rozen and Alexander were dealing with a group that is probably not monophyletic, Roig-Alsina's (1991) analysis should be considered the best available hypothesis of the phylogenetic position of *Nomada*. Nevertheless, it should be noted that the taxon identified in this analysis as *Nomada's* sister group, the tribe Biastini, shares only one synapomorphy, a reduction in the amount of sclerotization of S6 in females.

The Data Matrix. Analysis 1 used 20 subgroups of *Nomada* and 34 characters, with character polarities determined by application of Maddison et al.'s character optimization method to Roig-Alsina's cladogram for the Nomadinae. (Roig-Alsina actually presented two cladograms, which differed only in the placement of one genus. Either tree supported the same polarity decisions.) This procedure resulted in decisive polarity decisions for 30 of the 34 characters. The characters and their alternate states are listed and briefly described in Table 1, and the data matrix of Table 2 shows the *Nomada* subgroups and the states of each character for

each subgroup, thus providing a tabulated description of each subgroup. The character codings for the "hypothetical outgroup" taxon in Table 2 indicate the inferred polarity of each character and identify the four characters (#14, 15, 21, and 25) for which polarity decisions were equivocal. Eight of the characters are common to both sexes, seven are restricted to females, and nineteen are restricted to males (fourteen of these male characters involve the genitalia and S7 and S8). Twenty-one characters are treated as nonadditive (Mickevich, 1982) because they are multistate characters for which I am unable to postulate, *a priori*, a single most logical transformation series. By coding these characters as nonadditive, a postulated transformation series is determined by the best fit of these characters to the branching pattern based upon the most parsimonious distribution of the other characters in the data set.

TABLE 1. LIST OF CHARACTERS AND CHARACTER STATES USED IN THE CLADISTIC ANALYSES. More complete descriptions of character states are found in the text. Characters marked with an asterisk are coded as nonadditive. Shown in brackets after the descriptions of the states for each character are the weights assigned to the character after the first and last iterations of the successive approximations weighting procedure in Analyses 1 and 2. Thus, the designation [3,3] [2,1] for Character 5 means that this character received a weight of 3 on both the first and last iterations of Analysis 1, whereas in Analysis 2 its weight after the first iteration was 2 and its final weight was 1. *Brachynomada* group is equivalent to Tribe Brachynomadini of Roig-Alsina and Michener (1993).

1. Base of proboscideal fossa: 0. Broadly rounded (Figure 32); **1.** Distinctly narrowed (Figure 30). [0,0] [0,0].

***2. Malar space: 0.** Open anteriorly, closed posteriorly (Figure 34); **1.** Open anteriorly and posteriorly (Figure 35); **2.** Closed anteriorly and posteriorly. [10, 10] [0,0].

3. Anterior margin of pronotum: 0. Evenly rounded in profile (Figure 38); **1.** Distinctly angulate in profile (Figure 36). [10,10] [10,10].

4. Metapleuron: 0. Not protuberant above; **1.** Protuberant above (Figure 38). [10,10] [0,0].

***5. Sculpturing of propodeal enclosure: 0.** Very finely sculptured throughout, appearing granulose, shagreened, or with extremely fine rugulae in a "fingerprint" pattern (Figures 40,41); **1.** Rugose or reticulate basally, granulose or shagreened apically (Figures 39,43); **2.** Rugose or reticulate basally, polished apically; **3.** Rugose or reticulate throughout (Figure 42); **4.** Polished throughout. [3,3] [2,1].

6. Procoxal spine: 0. Absent; **1.** Present (Figures 44-47). [2,0] [2,0].

7. Lateral carina on procoxa: 0. Absent; **1.** Present near articulation with trochanter, fading out above; **2.** Present, complete. [2,2] [1,1].

8. Apex of marginal cell: 0. Pointed or very narrowly rounded (Figures 49,50); **1.** Broadly rounded (Figure 48); **2.** Obliquely truncate. [0,0] [2,1].

9. Female paraocular ridge: 0. Absent (Figure 51); **1.** Present (Figure 52). [0,0] [1,1].

***10. Female metasomal sternum 5 (S5): 0.** Unmodified; **1.** Apically emarginate, with a pair of tufts of stout, bristlelike setae (Figure 1); **2.** Apically produced, with a setal tuft on the process (*Brachynomada* group, Figure 7a in Alexander, 1990); **3.** Broadly U-shaped in cross-section (Figure 5a in Alexander, 1990); **4.** Apically emarginate, with subapical fringe of flexible plumose setae (*Ammobatoides*). [10,10] [10,6].

***11. Female T5: 0.** Unmodified, no prepygidial fimbria ("pseudopygidium"); **1.** "Typical *Nomada*" pseudopygidium (Figure 6, see text); **2.** No specialized setae, but a pair of cuticular denticles (*odontophora* group); **3.** A dense, velvety patch of short setae (*Brachynomada* group); **4.** Apicomedian tubercle with dense mat of reflective setae (*Hexepeolus*, Epeolini, Biastini); **5.** (Ammobatoidini); **6.** Apex with median emargination, but no specially modified setae (Neolarrini); **7.** A pair of spinelike processes (Caenoprosopidini). [10,10] [10,10].

***12. Female S6** (detailed descriptions of outgroup states in Roig-Alsina, 1991, abbreviated as RA in list below): **0.** Unmodified; **1.** Truncate apically, with apicolateral tufts of stout, clawlike setae (*Nomada*: Figures 2,3; RA Figure 4); **2.** (*Brachynomada* group: Figure 4; RA Figures 1,9); **3.** (*Hexepeolus*: RA Figure 11); **4.** (Ammobatoidini, Epeolini: RA Figures 7,8,10); **5.** (Biastini: RA Figures 5,6,21,22); **6.** (*Townsendiella*: RA Figure 3); **7.** Apex deeply emarginate, lateral lobes narrow, without spinose or bladelike setae (*Neolarra*: RA Figures 12,13); **8.** A single narrow, apically bifid median process (Ammobatini: RA Figure 2). [10,10] [10,10].

13. Female T6: 0. Without a tuft of bristlelike setae laterad of base of pygidial plate; **1.** With such a pair of tufts of setae (Figure 5). [10,10] [10,10].

14*. Female pygidial plate: 0. Narrowly rounded apically (Figure 59); **1.** Broadly rounded apically (Figure 60); **2.** Truncate apically; **3.** No plate, apex of T6 deeply emarginate, bearing a distinct setal fringe (Biastini); **4.** Plate with apicomedian emargination (*Neolarra*); **5.** No plate, apicomedian felt-like patch of setae (Ammobatini). [2,2] [4,4].

***15. Apicomedian setae on female hind tibia: 0.** Absent; **1.** Stout, spinose, cylindrical or flattened (Figure 53); **2.** Short, stout, peglike, heavily melanized (Figure 55); **3.** Flattened area bearing a dense cluster of stout, straight, flattened setae (Figure 54); **4.** Long, narrow, in a dense cluster of ca. 10-25 setae (Figures 56,57); **5.** Broad, flat, bladelike, apically curved, imbricate (Figure 58). [10,10] [6,6].

16. Scape of male antenna: 0. Cylindrical (or slightly flattened in *Brachynomada* group), not conspicuously wider than flagellum; **1.** Cylindrical, conspicuously wider than flagellum; **2.** Greatly enlarged, subglobose.

17. Male oblique frontal ridge: 0. Absent; **1.** Present (Figure 33). [10,10] [10,10].

***18. Base of male hind femur: 0.** Without any specially modified setae; **1.** Femur with shallow ventral depression and flocculus of long, plumose setae (Figure 67); **2.** Tuft of long, erect setae on trochanter, depression with dense patch of recumbent setae on femur (Figure 68); **3.** Anterior and posterior margin of ventral face of femur with row of long, plumose setae (Figure 65). [10,10] [10,10].

***19. Male subgenital brush: 0.** Absent; **1.** Setae very short and simple ; **2.** Setae longer, suberect mesally and semi-recumbent laterally (Figure 7b); **3.** Median tuft absent or extremely sparse, lateral tufts dense, well developed (Figure 7g); **4.** Setae long, erect, often recurved apically (Figures 7a,c,d); **5.** Setae long, erect, plumose, densely clustered, either with two closely-spaced tufts or merging into a single dense tuft (Figures 7e,f, 69); **6.** Setae long, dense, plumose, horizontally directed, forming an apical fringe along margin of sternum 6 (Figure 7h). [7,7] [7,7].

***20. Male S7: 0.** Apodemes moderately long, disc of sternum subtriangular, apical margin broadly to narrowly rounded or subtruncate (Figures 73-75); **1.** Apodemes long and narrow, "disc" of sternum narrowed to an apicomedian process that is rectangular or has concave sides (*integra* group, Figures 107-109); **2.** Apodemes as in state 0, but apex modified into a broad, spatulate structure (*gigas*, Figures 100-101); **3.** Overall shape as in state 0, but apical margin laterally compressed, sometimes also strongly recurved or bearing a ventromedian keel (*armata* group); **4.** Apodemes very long and narrow, median process long, narrow, parallel-sided (*Brachynomada* group); **5.** Apodemes narrow but relatively short, disc of sternum broad and flat, constricted near base (Epeolini); **6.** Apodemes moderately long, disc subtriangular, apical margin strongly recurved (*Biastes*); **7.** Apodemes moderately long, "disc" reduced to a transverse strap (Caenoprosopidini). [10,10] [10,10].

***21. Median process on male S8: 0.** Not present; **1.** Dorsoventrally compressed, short and broad, apex broadly rounded (Figure 76); **2.** Dorsoventrally compressed, long and narrow, apex

TABLE 1. (continued)

narrowly rounded (Figures 77-78); **3.** Laterally compressed, long, narrow, parallel-sided, often expanded apically (Figures 80-83); **4.** Laterally compressed and more or less parallel-sided, as in state 3, but very short, distinctly expanded apically (Figure 79); **5.** Laterally compressed, tapering from broad base to truncate, recurved apex (*rodecki*, Figure 104 in Mitchell, 1962); **6.** Long, narrow, parallel-sided, subtriangular in cross section (*Neopasites*); **7.** Dorsoventrally compressed, parallel-sided, apex broadly rounded (some *Biastes* and Ammobatini). [4,2] [5,4].

22. Spinose setae on median process of male S8: 0. Absent; **1.** Present (Figures 76-78). [10,10] [10,10].

***23. Shape of male gonostylus: 0.** Cylindrical, long, narrow, apex rounded but not expanded (Figures 87,98,117,121,127,136-141); **1.** Narrow and cylindrical apically, tip somewhat swollen; **2.** Cylindrical, short, broad, apex blunt and rounded (Figures 86,88-91); **3.** Flattened or subtriangular in cross section, apical portion often curved toward midline of genital capsule (Figures 110-116); **4.** Cylindrical, long, narrow, strongly curved mesad (Figures 172,173); **5.** As in *bifasciata* group (Figures 166-168); **6.** As in *basalis* group (Figures 149-152,154-155,157-159); **7.** Broad, flat, curved weakly mesad (*Neopasites*, some *Biastes*); **8.** Broad, fused with gonocoxite (*Caenoprosopis*). [10,10] [10,10].

***24. Shelf on inner base of male gonostylus: 0.** Absent; **1.** Present, not bearing any specialized setae; **2.** Present, with a few short, stout, melanized setae (Figures 90-91,145). [5,5] [5,5].

***25. Vestiture of male gonostylus: 0.** Sparse, simple, some setae more than half as long as gonostylus (Figures 133-135,136-141); **1.** Sparse, simple, setae less than half as long as gonostylus (Figures 87,121-123,127-128); **2.** Sparse and simple as in state 0, but arising only from apex and ventral face of gonostylus (Figures 130-132); **3.** Very long, dense, apically plumose or sinuate (Figures 86,88-91); **4.** As in state 3, but divided into basal and apical tufts (Figures 172-174); **5.** As in state 5, but apical tuft subdivided (Figures 166-168). [10,10] [6,4].

***26. Ventral hook on penis valve: 0.** None present; **1.** Present as a single hook-shaped process near apical third of valve (Figures 93,122-123,127); **2.** An angulate projection near apical third of valve (*Hexepeolus*); **3.** A hook-shaped process in basal half of valve (Epeolini: Figure 5g,h,i in Alexander, 1990). [10,10] [10,10].

***27. Invagination of dorsal gonocoxite: 0.** Absent; **1.** Present (Figure 88); **2.** *gigas*: median sinus broadly V-shaped, invagination extremely shallow or absent (Figure 98); **3.** *Hexepeolus*: mesal face of gonocoxite with a right-angle bend. [10,10] [10,10].

***28. Inner dorsal lobe of gonocoxite: 0.** Absent or very weak (Figure 130); **1.** Present, about as long as broad (Figures 88,90); **2.** Present, much longer than broad (Figure 133); **3.** Present, much broader than long (Figure 121); **4.** *Hexepeolus*: mesal face of gonocoxite with a right-angle bend. [10,10] [10,10].

29. Sclerotized patch on mesal face of gonostylus: 0. Absent (Figures 143,145); **1.** Present (Figure 148). [10,10] [10,10].

***30. Subapical setal fringe on metasomal sterna: 0.** Absent; **1.** Composed of long, erect, flexible setae (Figures 7e,f); **2.** Epeolini: long, dense, recumbent setae on S4 and S5; **3.** *Hexepeolus*: short, flexible, recumbent, densely plumose. [0,0] [0,0].

31. Inner ridge on penis valve: 0. Absent (Figures 88,96); **1.** Present (Figures 93,124-126,129). [10,10] [10,10].

***32. Outer lateral ridge on penis valve: 0.** Absent (Figure 96,97); **1.** Present, broadly rounded, more or less welt-like (Figure 93); **2.** Present, angulate or carinate, penis valve subtriangular in cross section (Figures 92,94,95); **3.** Present as a carinate sinuous ridge (*gigas*, Figures 98,99). [10,6] [10,6].

***33. Basoventral lobe on gonostylus: 0.** Absent (Figures 131,132,134,135); **1.** Present, more or less hemispherical (Figures 99, 122,123); **2.** Present, more or less cylindrical (Figure 90,91); **3.** Present, transverse ridge (Figure 173). [4,4] [2,2].

34. Basoventral setal tuft on gonostylus: 0. Absent (Figures 134,135); **1.** Present, setae short and simple, sparse (Figures 122,123); **2.** Present, setae dense, long, apically plumose or sinuate (Figures 142-145, 173-174). [4,4] [3,2].

The analyses presented here were done on a Zenith 386 personal computer using the Hennig86 program, Version 1.5 (Farris, 1988), which employs parsimony methods. The "mhennig*" command was used to locate a minimum length cladogram, and this was followed by extensive branch swapping (the "bb*" command) on this cladogram to locate all minimum-length cladograms.

Results of Analysis that Weighted All Characters Equally. This analysis found 35 equally parsimonious cladograms, each with a length of 96 steps, a consistency index of 71, and a retention index of 69. A strict consensus tree (Figure 8) shows two polytomies, labelled as nodes A and B. There are seven equally parsimonious resolutions of the polytomy at node A (Figure 10) and five resolutions of the polytomy at node B (Figure 9).

The seven competing resolutions at node A involve alternative placements of two taxa, the *erigeronis* group and the *integra* group. The *erigeronis* group is either the sister group of the South African species *Nomada gigas* (trees A1-A4 in Figure 10), or it is the sister group of a clade comprising the *vegana* and *roberjeotiana* groups (trees A5-A7). There are three possible placements of the *integra* group relative to other lineages: trees A1 and A5 in Figure 10 represent one placement, trees A2, A4, and A6 represent another, and trees A3 and A7 represent the third.

The only putative synapomorphy shared by the *erigeronis* group and *gigas* is a type of propodeal sculpturing (character state 5-1) that is also found in several other groups within *Nomada* (the consensus tree in Figure 8 shows this same character state arising independently in the *vincta* group and the taxa involved in the polytomy at node B). This placement of the *erigeronis* group also involves the hypothesis that the absence of an invagination and inner dorsal lobe on the gonocoxite (character states 27-0 and 28-0) is a primitive absence rather than a secondary loss in the *erigeronis* group. A sister group relationship between the *erigeronis* group and the *roberjeotiana-vegana* clade is likewise supported by only one putative synapomorphy, the presence of a spinose process on the procoxa (character 6). This process is not present in all species of the *roberjeotiana* group, and similar processes occur in other groups, such as the *odontophora* group and in a few species of the *ruficornis* group (e.g Figure 44). However, the *erigeronis* group also shares distinctive modifications of the male genitalia and associated sterna (character states 21-1 and 32-2) with the *elegantula* and *abyssinica* groups as well as the *vegana* and *roberjeotiana* groups. These character states do not occur in any other *Nomada* or in the outgroup, so I would consider them more plausible candidates as true homologies. Furthermore, placement of the *erigeronis* group within this clade implies that the elaborate subgenital brush of this group (character state 19-5, Figures 7e,f) is derived from a similar but less elaborate brush common in many members of the *vegana*, *roberjeotiana*, *elegantula*, and *abyssinica* groups (character state 19-4, Figures 7c,d). Although the form of the subgenital brush is by no means uniform within this putative clade and hypotheses about sequences of change in its form are highly speculative, it seems more plausible that the elaborate structure of the *erigeronis* group arose from some precursor represented by the forms coded as having state 19-4 than that it arose *de novo*, which is the implied hypothesis if the *erigeronis* group is the sister group of *Nomada gigas*.

TABLE 2. DATA MATRIX FOR CLADISTIC ANALYSES. Characters are defined in Table 1. A – in a cell indicates that the state for the character varies within the taxon; a ? indicates that the state is unknown for the taxon (because the taxon is only known from one sex). The *Brachynomada* group is as defined in Roig-Alsina (1991); it is equivalent to Brachynomadini of Roig-Alsina and Michener (1993).

	CHARACTER						
	1	11111	11112	22222	22223	3333	
TAXON	12345	67890	12345	67890	12345	67890	1234
Biastes	00001	00100	45031	0000-	-0-00	00000	00--
Neopasites	0200-	00100	45031	00000	60701	00000	0000
Townsendiella	00000	00103	06010	00000	00?01	00000	0022
Hexepeolus	00001	00100	43020	00000	00730	33404	0001
Ammobatoidini	0-00-	0110-	540-1	00000	00-0-	0000-	0000
Neolarra	00-01	00103	67040	00000	00001	00000	0000
Caenoprosopis	02010	00200	07041	00007	30801	00000	0000
Ammobatini	-000-	00213	08051	0000-	-0001	00000	00--
Brachynomada group	0-000	0-0-2	320-0	00004	-000-	00000	00--
Epeolini	00000	0-013	440-0	00005	00-00	20003	0000
Hypothetical Outgroup	00000	00100	400--	00000	-000-	00000	0000
elegantula group	0000-	00011	11101	00040	11000	01100	0200
roberjeotiana group	00100	-0011	11101	000-0	11000	01100	0200
vincta group	00001	00011	11101	-0010	21001	11300	1111
odontophora group	10000	12101	21101	00010	31021	11100	1101
vegana group	101-0	1-101	111-1	00040	21-00	01200	0200
adducta group	00000	00011	11101	-0010	21001	01100	0000
abyssinica group	0000-	00011	11101	00040	11000	0110-	0200
gigas	00001	00011	11101	00002	31000	02000	0312
erigeronis group	00011	10011	11101	10050	11-02	00001	020-
rodecki	00000	001??	?????	0001?	51203	01100	0022
integra group	000-2	00011	11101	00-21	31300	01100	0000
trispinosa group	00001	01011	11112	003-0	31414	01100	0032
furva group	-000-	00011	11101	-0-30	41414	01100	0032
fuscicornis group	10001	00011	11103	-112-	31203	01110	00-2
armata group	00001	00011	1110-	-1123	31202	01110	00-2
ruficornis group	00001	0-011	11101	-0020	31213	01100	0022
belfragei group	00000	01101	11101	00020	31223	01100	0012
superba group	0100-	01011	11114	00020	31223	0110-	0022
basalis group	0-00-	01011	11114	00020	316-3	01-01	00-2
bifasciata group	00001	00011	11105	-0260	315-5	01100	0022

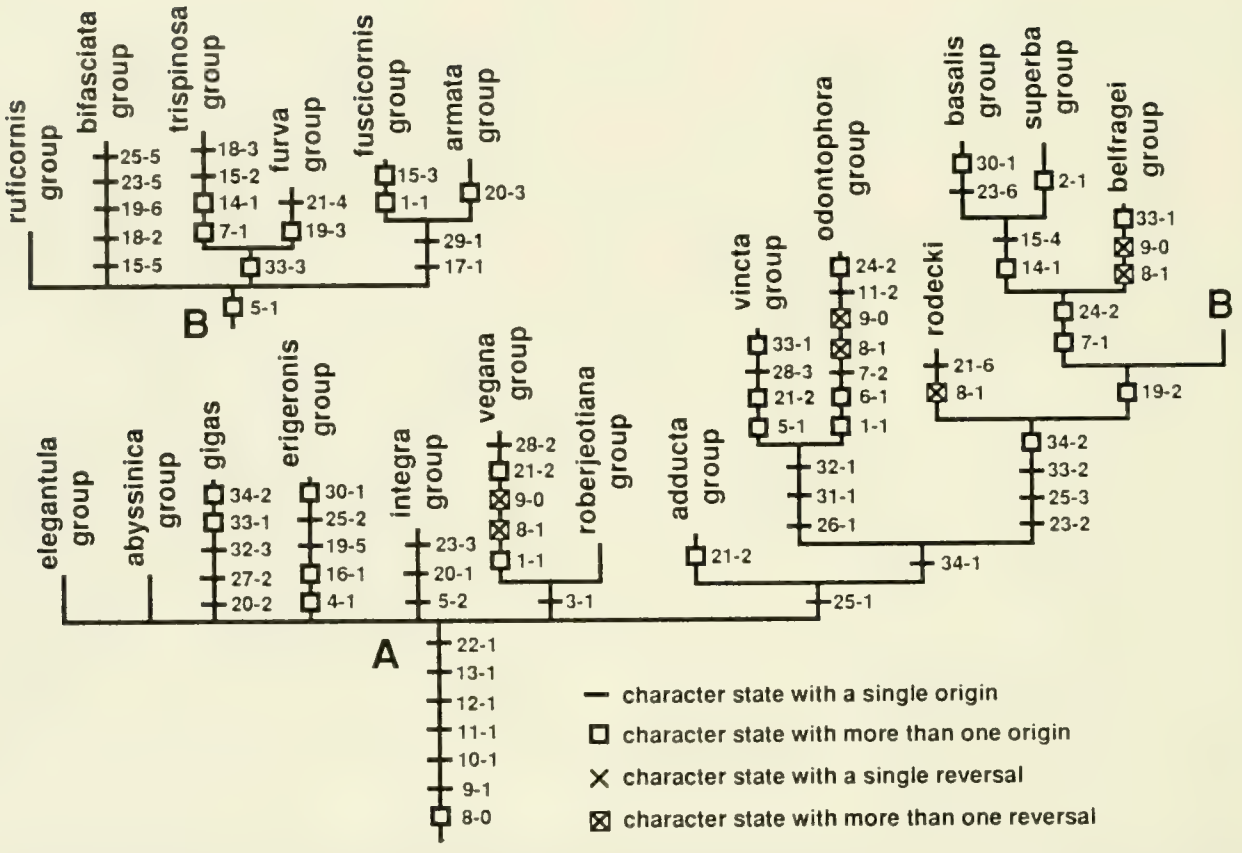


Fig. 8. Strict consensus tree for the thirty-five equally parsimonious trees found in Analysis 1 when all characters were given equal weight. Only characters whose distribution is the same on all thirty-five trees are shown on this cladogram. Figs. 9 and 10 show the distribution of characters that support conflicting resolutions of the polytomies at nodes A and B.

The alternative placements of the *integra* group also involve different interpretations of the sequence of transformations in the subgenital brush, as well as competing hypotheses of the ancestral condition for the median process of S8 (character 21, one of the four characters for which the polarization procedure used in Analysis 1 produced equivocal results). The subgenital brush in the *integra* group resembles that of groups higher up in the cladogram (above *rodecki* in the consensus tree of Figure 8), rather than any of the other groups involved in the polytomy at node A. I see no strong basis for favoring any one of the three alternative placements of the *integra* group in Figure 10.

Two of the five resolutions at node B can be rejected on grounds of parsimony. The *bifasciata* group is coded as variable for character 24 (shelf on inner base of gonostylus), because states 1 and 2 occur in this group. Because Hennig86 does not have a way of specifying that some, but not all, states of a multistate occur in a taxon, it may produce cladograms that imply groundplan states that do not actually exist within a taxon. Trees B3 and B5 exemplify this problem. They hypothesize that the common ancestor of the *bifasciata* group and its closest relatives had state 24-0, yet a change to an alternate state (either 24-1 or 24-2) within the *bifasciata* group is not detected by Hennig86 and thus not counted as an additional step in comparing lengths of different trees. If this undetected extra step is taken into account, trees B3 and B5 are one step longer than the other three trees.

Tree B1 might also be questioned on the grounds of the hypothesis of character change that it implies. The common ancestor of the clade containing the *bifasciata, ruficornis, trispinosa,* and *furva* groups is shown with two states for character 24. (Character states for inner branches on the cladograms were obtained by using the "xsteps h" command in Hennig86.) Mathematically, the assignment of more than one state to an internal branch means that either state at that position results in a tree of equal length. Two biological interpretations can be given to the assignment of two (or more) states to a hypothetical ancestor. One interpretation is that it is not possible to determine which of the states was fixed in the ancestor (because either possibility results in an equally parsimonious tree); the other is that the ancestor was polymorphic for the character. Under the latter interpretation, assignment of a single state on a branch higher up on the cladogram can be interpreted as the fixation in a descendant of one of the alternate states that was present in a polymorphic ancestor. Such a history of character evolution is certainly consistent with evolutionary theory, but it raises questions about what kind of character change should count as a "step" in the arithmetic of counting and comparing tree lengths. In tree B1, the development of a polymorphism in character 24 is *not* counted as a step

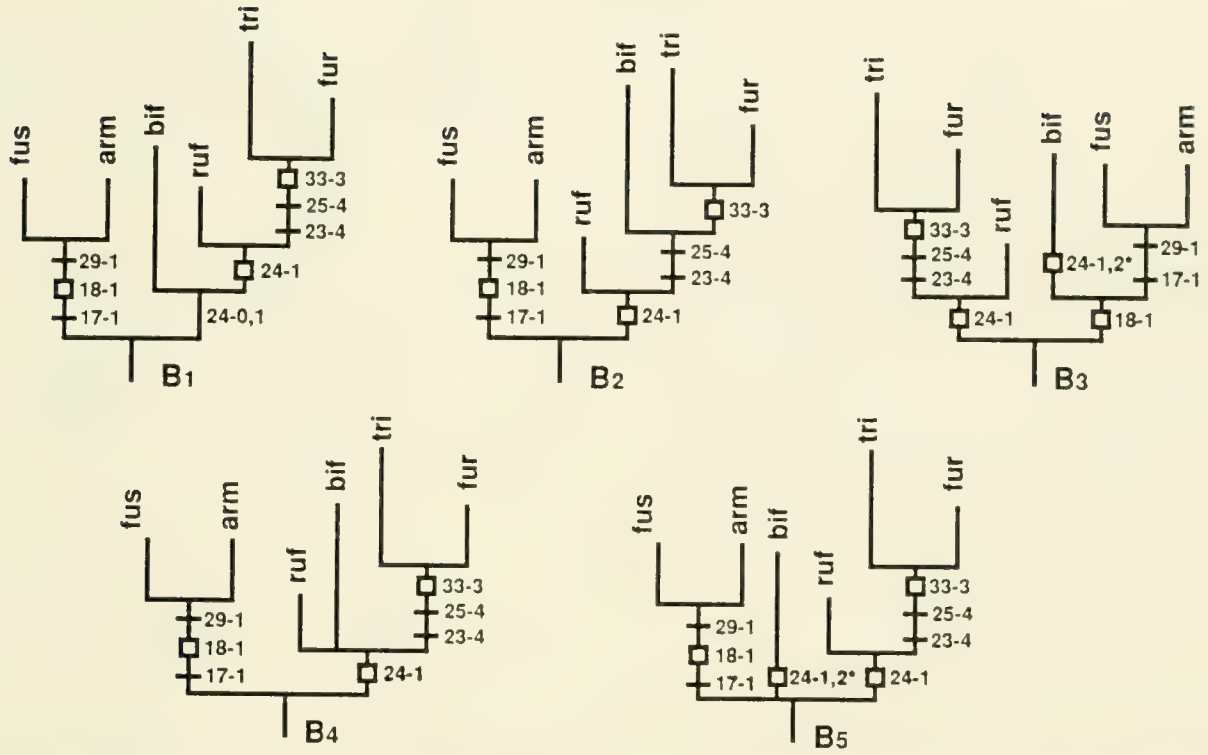


Fig. 9. The five equally parsimonious resolutions of the polytomy at node B of Fig. 8. Only the characters involved in different resolutions of the polytomy are mapped onto these cladograms. Species group names are abbreviated with the first three letters of the names shown in Fig. 8. Horizontal bars depict character states with a single origin, open squares depict character states with more than one origin (either among these six taxa or elsewhere on the tree), and internal branches with more than one state depicted for a character are discussed in the text.

by the Hennig86 program, whereas the subsequent fixation of state 1 in the common ancestor of the *ruficornis*, *trispinosa*, and *furva* groups *is* counted as one step.

The alternative interpretation of the assignment of more than one state to a character on an internal branch, *viz.* that it signifies uncertainty rather than a hypothesis about a polymorphic population, seems to mean that there is not actually any character state supporting that branch on the cladogram (or, alternatively, if the character *does* change at that branch, it cannot *also* count as a synapomorphy at a higher branch on the same cladogram). What this means for tree B1 is that if the change from state 24-0 to state 24-1 is only to be counted one time, one of the two branches at the base of the *bifasciata-furva* clade has to be collapsed. This would make tree B1 identical to either B4 or B5.

Thus, a careful assessment of the way tree lengths are determined suggests that the number of "equally parsimonious" trees at node B can be reduced to two, represented by trees B2 and B4. The topological difference between the two is that tree B4 has an unresolved trichotomy that is resolved in tree B2. This is a consequence of different interpretations of the sequence of changes in the shape and vestiture of the gonostylus (Figure 11). Tree B2 (Figure 11a) hypothesizes that the gonostylus of the *bifasciata* group (character states 23-5 and 25-5) is derived from an ancestral condition like that found in the *trispinosa* and *furva* groups (character states 23-4 and 25-4). Tree B4 (Figure 11b) hypothesizes that the distinctive gonostyli of the *bifasciata* group and the *trispinosa-furva* clade were independently derived from an ancestor with character states 23-2 and 25-3. Neither hypothesis can be rejected out of hand, although I am inclined to favor that represented by Figure 11a on the grounds that the shape and vestiture of the gonostylus in the *trispinosa* and *furva* groups appears to be a plausible intermediate between that of the *bifasciata* group and the form that is considered ancestral under either hypothesis. Specific features that seem intermediate are the strong curvature of the gonostylus toward the midline of the genital capsule, and the separation of the vestiture into distinct basal and apical tufts.

Results of Analysis with Successive Approximations Character Weighting. Another way of evaluating the numerous competing phylogenetic hypotheses of Analysis 1 is to apply an objective and explicit method of assigning differential weights to characters. Successive approximations character weighting (Farris, 1969) is a procedure in which weights are assigned to characters on the basis of their level of homoplasy on an initial cladogram (or cladograms) obtained by a parsimony analysis that gives all characters equal weight. The specific weighting function employed by Hennig86 ("xsteps w" command) is the best fit according to the rescaled consistency index (Swofford, 1993; p. 55). The weighted characters are then subjected to a parsimony analysis, and the weight for each character is recalculated according to its fit to this new cladogram (or cladograms). This procedure is continued until the weight for each character

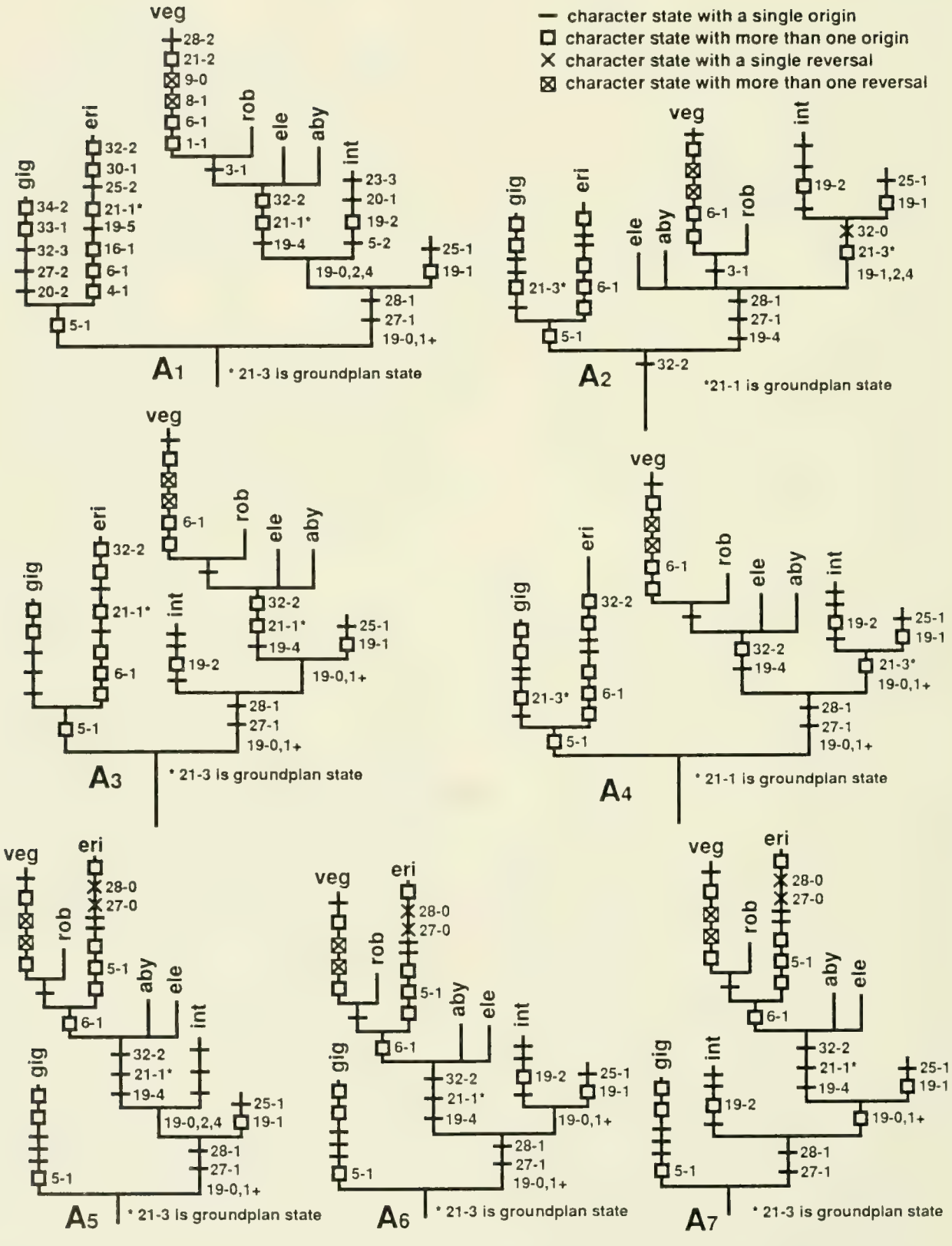


Fig. 10. The seven equally parsimonious resolutions at node A of Fig. 8 (Analysis 1). Tree A1 shows the distribution of all characters; other trees show only character distributions that differ from tree A1. Species group names are abbreviated with the first three letters of the names shown in Fig. 8.

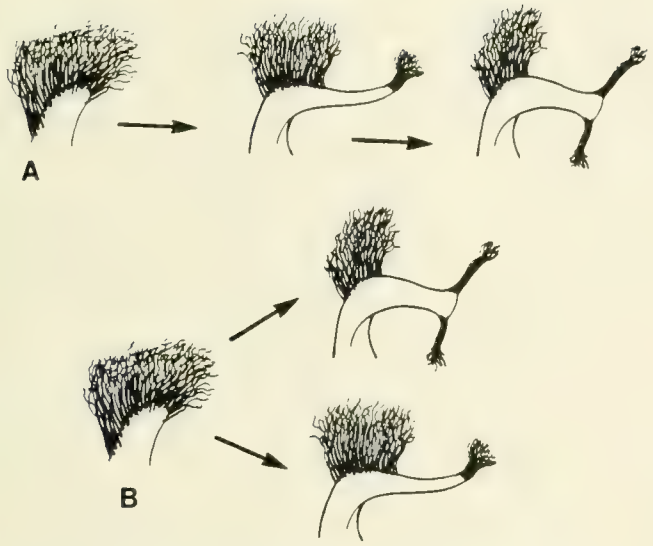


Fig. 11. (a) Hypothesized transformation series for gonostylus shape and vestiture as determined by optimized fit to tree B2 in Fig. 9; (b) Hypothesized transformation series for gonostylus shape and vestiture as determined by optimized fit to tree B4 in Fig. 9.

no longer changes between iterations, and at this point the resulting cladogram is inferred to be the best available phylogenetic hypothesis for the group under study.

Application of successive approximations character weighting to the data matrix of Analysis 1 results in 20 equally parsimonious cladograms. The same five resolutions at node B that are found when all characters are given equal weight remain equally parsimonious after differential weights have been assigned by the successive approximations procedure. For node A, the four resolutions (trees A1-A4) that have the *erigeronis* group as the sister group of *gigas* are retained, whereas the three resolutions (trees A5-A7) that have the *erigeronis* group as the sister group of the *vegana-roberjeotiana* group clade are not supported.

An examination of the weights assigned to each character (Table 1) shows why trees A5-A7 are rejected by the successive approximations weighting procedure. It is especially noteworthy that the only characters whose weights were decreased in successive interations are characters 6, 21, and 32, precisely those characters that support the placement of the *erigeronis* group on the rejected trees. The putative synapomorphy of *gigas* and the *erigeronis* group, character 5-1, is given low weight by successive approximations, although it receives a slightly higher weight than character 6-1, the putative synapomorphy of the *erigeronis* group and the *vegana-roberjeotiana* group clade. A more compelling reason why the *erigeronis* group is placed with *gigas* at the base of the tree is that characters 27 (dorsal invagination of the gonocoxite) and 28 (inner dorsal lobe of the gonocoxite) are given the maximum possible weight, so that their reversal on trees A5-A7 would require twenty steps.

The independence of the latter two characters could be challenged on the grounds that they are artificially differentiated parts of a single continuous structure (in many cases they are roughly mirror images of one another). If they are not independent, treating them as two separate characters, each of which is assigned the maximum possible weight in a successive approximations analysis, could give them an inappropriately large influence in the cladistic analysis. A crude but simple test of the possible effect of the non-independence of these two characters is to do a parsimony analysis with only one of them. I chose to retain character 27 because, with the exception of an autapomorphic state in *Nomada gigas*, it exhibits only one derived state in the ingroup, whereas character 28 has two autapomorphic states within the ingroup. Apart from deleting character 28 from the analysis, all other elements of this analysis (designation of additive characters, tree-searching commands) were the same.

With all characters assigned equal weight, there were 1700 equally parsimonious trees, with a consistency index of 71 and a retention index of 69 (these indices were the same in the analysis with character 28 included). This very large number of equally parsimonious solutions is very similar to the result of Analysis 2 that will be presented below. Successive approximations character weighting reduces the number of equally parsimonious solutions to 98 trees, with a consistency index of 90 and a retention index of 88. A strict consensus tree for these 98 trees (Figure 12) is very similar to results obtained when character 28 is not excluded. Figure 12 has the same topology for all taxa above *rodecki* on Figure 8, including the polytomy at node B. The *odontophora* and *vincta* groups are sister taxa, and this clade is part of a trichotomy with the *adducta* group and the clade with *rodecki* as its basal component. The large basal polytomy at node A in Figure 8 is more fully resolved in this modified analysis, because the *erigeronis* group has only one position, as the sister group of *vegana* + *roberjeotiana*, as in trees A5 - A7 in Figure 10. *Nomada gigas* retains its basal position, and the *integra* group remains difficult to place decisively, although its position is somewhere near the base of the tree. In short, if the structures coded as characters 27 and 28 do not represent independent items of evidence concerning phylogenetic relationships, but are more appropriately considered a single item of evidence, the *erigeronis* group is placed within the *vegana-roberjeotiana* clade without substantially altering the position of other taxa on the cladogram.

Summary of Conclusions from Analysis 1. The thirty-five equally parsimonious trees that result when all characters are given equal weight involve seven possible resolutions at node A on Figure 8, and five possible resolutions at node B.

Three of the resolutions at node B can be rejected on grounds of parsimony when one considers cases of uncounted character change in the *bifasciata* group or a "polymorphic" ancestor. Of the remaining two resolutions, tree B2 is tentatively preferred on the grounds that it hypothesizes a more plausible sequence of changes in the form and vestiture of the gonostylus. Successive approximations character weighting does not alter conclusions about the resolution of node B.

The seven resolutions at node A involve two alternative placements of the *erigeronis* group and three alternative placements of the *integra* group. There is no strong basis for preferring any of the three placements for the *integra* group. The *erigeronis* group shares unique forms of male S8 and the penis valves with a clade consisting of the *abyssinica*, *elegantula*, *vegana*, and *roberjeotiana* groups, and the subgenital brush of the latter clade is a plausible precursor of the more elaborate structure in the *erigeronis* group. If these derived sim-

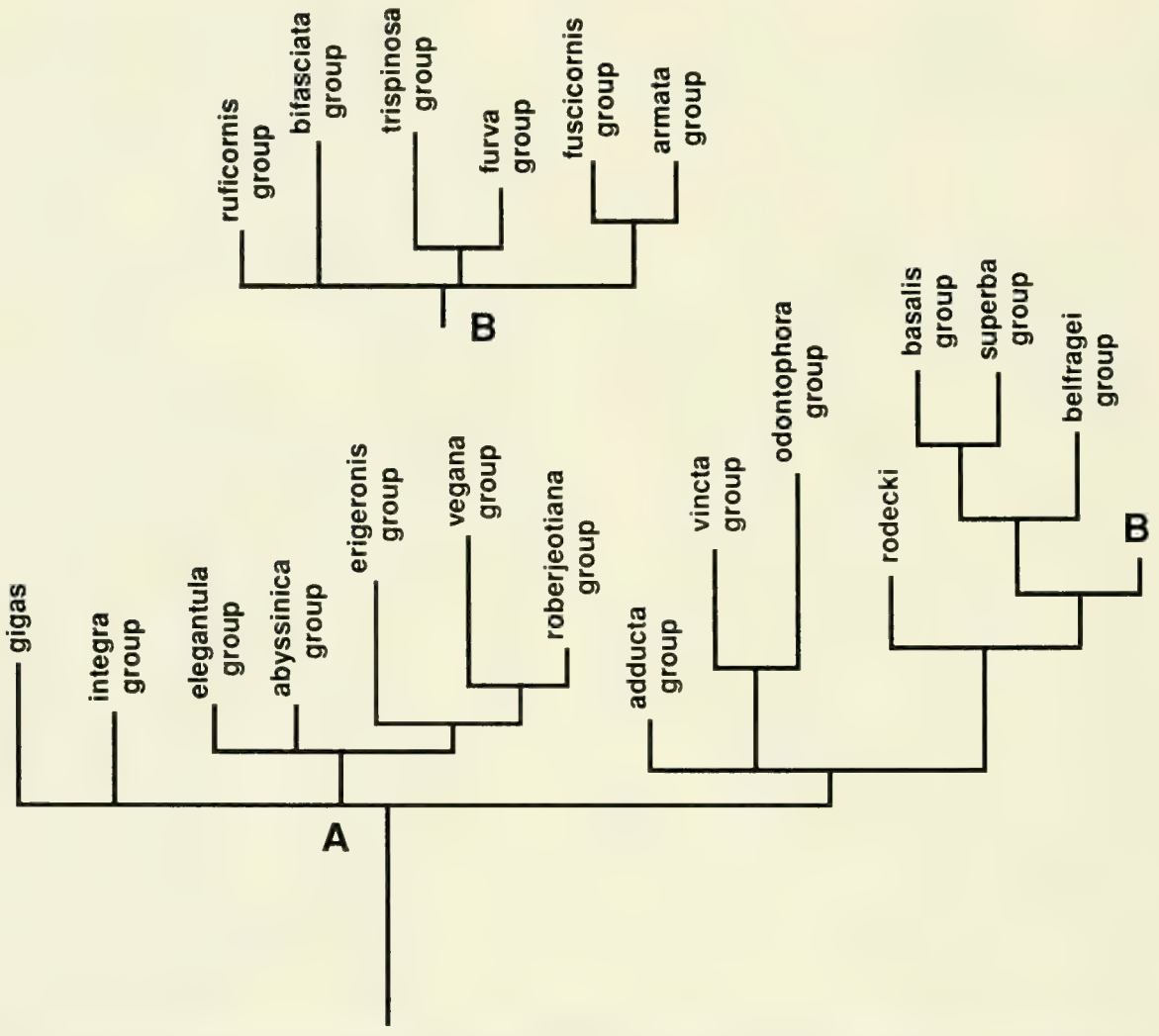


Fig. 12. Strict consensus tree for 98 equally parsimonious trees found after successive approximations character weighting when character 28 was omitted from Analysis 1.

ilarities are homologous, trees A5-A7 depict the proper phylogenetic position of the *erigeronis* group. However, placement of the *erigeronis* group in this clade requires the hypothesis that the dorsal invagination and inner dorsal lobe on the gonocoxite have been lost, and that the similar sculpturing of the propodeal enclosure in the *erigeronis* group and *Nomada gigas* is homoplastic.

I consider the placement of the *erigeronis* group in trees A5-A7 more plausible than its placement in trees A1-A4, on the grounds that the independent derivation of three distinct features of the male terminalia seems less likely than the loss of one pair of interrelated structures. The propodeal sculpturing shared by the *erigeronis* group and *gigas* is also present in many other groups of *Nomada*. Nevertheless, successive approximations character weighting favors the placement of the *erigeronis* group as the sister group of *Nomada gigas* (trees A1-A4).

Several terminal taxa used in this analysis are probably paraphyletic. With or without the *erigeronis* group, the *abyssinica, elegantula, vegana*, and *roberjeotiana* groups comprise a single well-supported clade. Within this clade, the *vegana* group is characterized by numerous autapomorphies, but none of the other three groups has its own unique derived characters. Another major group with no defining autapomorphies is the *ruficornis* group. The *armata* group is probably paraphyletic with respect to the *fuscicornis* group. Character 20-3 (form of male S7) is shown as an autapomorphy for the group, but the same state occurs in some species of the *fuscicornis* group, which was coded as variable for this character.

Analysis 2: Ten Nomadine Taxa as an Outgroup.

An alternative approach to character polarization is not to reconstruct a hypothetical ancestor, or ingroup groundplan, on the basis of a pre-existing hypothesis of phylogenetic relationships in the outgroup, but to include several outgroup taxa in the original data matrix and specify that these taxa be treated as the outgroup in order to root the tree. With this procedure, cladistic relationships among

the outgroup taxa are determined by the same characters that are used to resolve relationships within the ingroup. In cases where there is no well-corroborated cladistic hypothesis for the outgroup, one has little choice but to employ this method for polarizing ingroup characters. In the case of *Nomada*, there is an available cladogram based upon a rigorous phylogenetic analysis, but the evidence for the placement of *Nomada* on that cladogram is rather weak. Consequently, Analysis 2 was performed to determine how sensitive the conclusions of Analysis 1 are to the resolution of cladistic relationships in the outgroup.

The characters and taxa used in Analysis 2 were the same as for the first analysis (see Appendix and Tables 1 and 2). However, instead of mapping the character states of the outgroup taxa onto Roig-Alsina's cladogram for the Nomadinae, the "hypothetical outgroup" of Analysis 1 was removed from the data matrix, and in its place were substituted the ten taxa of Nomadinae shown in Table 2 and the Appendix. These ten taxa were designated as the outgroup for tree-rooting purposes. With the exception of the Biastini, tribes with more than one genus were treated as a single terminal taxon whose character state codings represent the estimated groundplan state for the tribe. The two genera of Biastini were treated as separate terminal taxa because they have different states for several characters and they belong to the tribe that Roig-Alsina has hypothesized to be the sister group of *Nomada*. Additivity codings and tree-finding commands were the same as for Analysis 1.

An initial run with all characters given equal weight found 1,723 minimum length trees, with a length of 146 steps, a consistency index of 69, and a retention index of 76. A strict consensus tree (Figure 13) shows *Nomada* to be monophyletic and a few consistent groupings within the genus, but no consistent resolution of outgroup taxa. What this means for character polarization is that any character exhibiting more than one state in the outgroup cannot be decisively polarized (Maddison et al., 1984).

Successive approximations character weighting considerably improved the resolution in the outgroup as well as the ingroup, and reduced the number of equally parsimonious trees to 98 (length = 758 steps, consistency index = 87, retention index = 98). A strict consensus tree for these 98 trees (Figure 14) shows that they involve multiple resolutions at three nodes. Node A involves the outgroup taxa *Neolarra* and *Townsendiella*, for which three arrangements (trees A, A1, and A2 on Figure 14) are equally parsimonious. Hypotheses of relationships within *Nomada* are the same with any of the three topologies. Node C is identical to node B

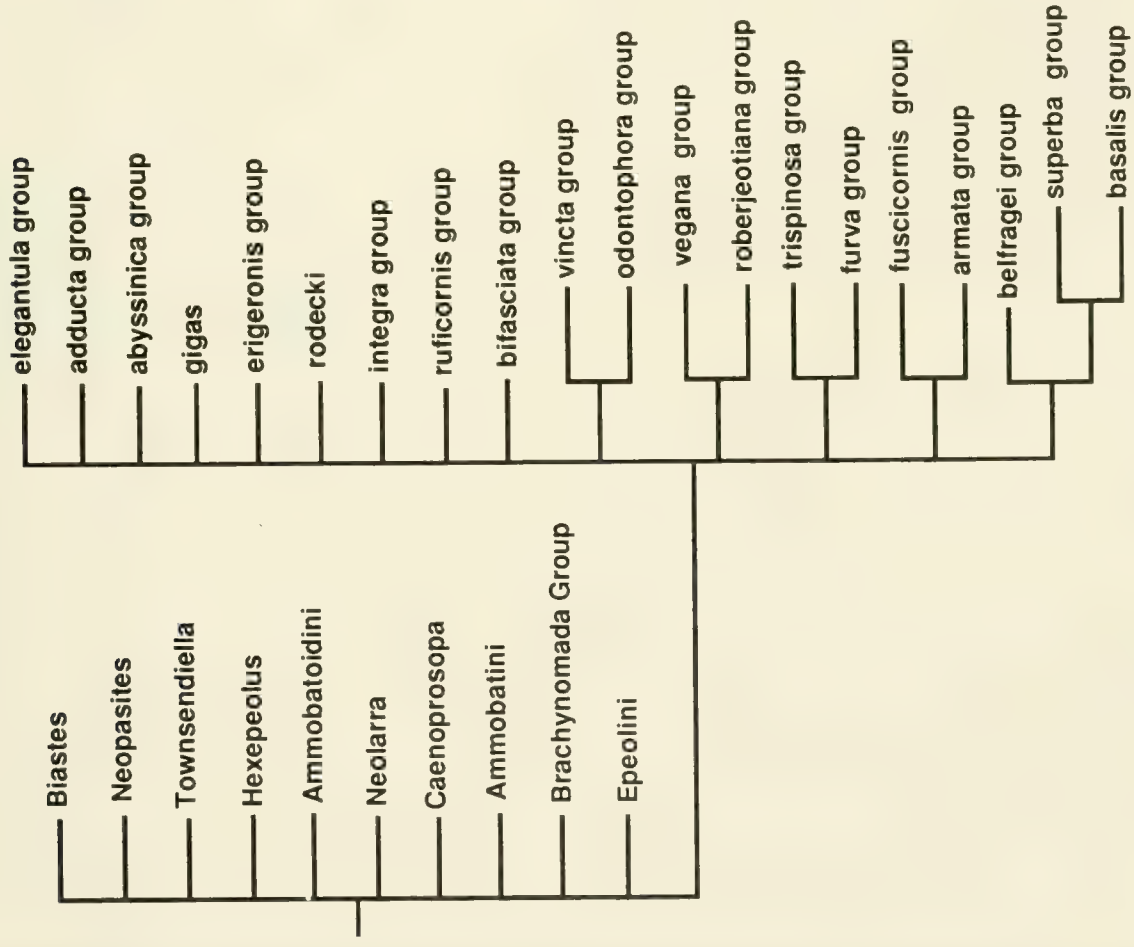


Fig. 13. Strict consensus tree for the 1,723 equally parsimonious trees found in Analysis 2 when all characters were given equal weight.

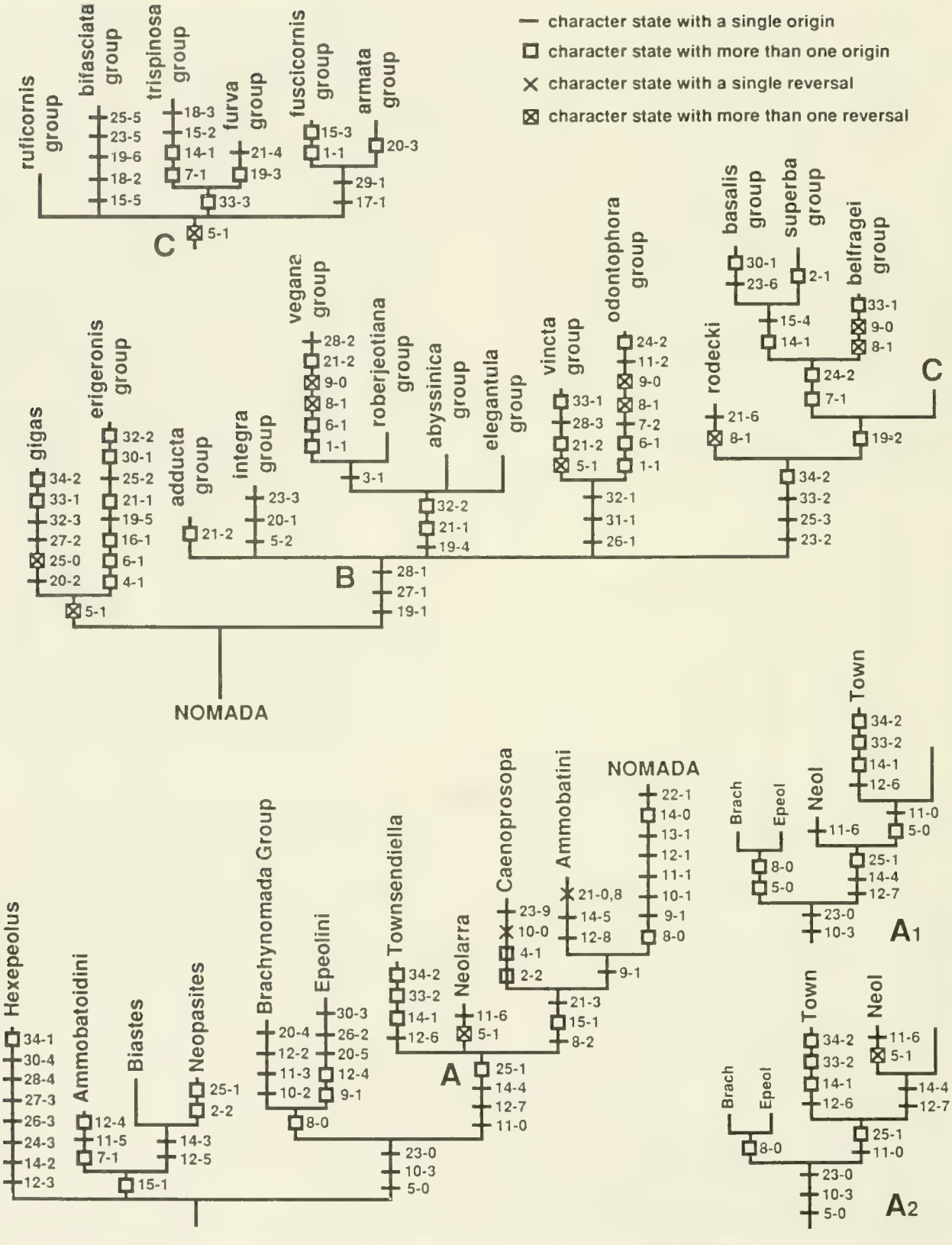


Fig. 14. Strict consensus tree for the ninety-eight equally parsimonious trees found in Analysis 2 when characters were weighted by the successive approximations procedure. Only those characters whose distributions are the same on all ninety-eight trees are shown on this cladogram. Other characters are shown on Figs. 10 and 15. Alternative resolutions of polytomy at node A are shown as trees A1 and A2. Abbreviations on these two trees: Town = *Townsendiella*, Neol = *Neolarra*, Brach = *Brachynomada* Group, Epeol = Epeolini.

from Analysis 1, and is resolved in exactly the same way in this analysis. There are seven equally parsimonious resolutions of node B. Three of these are identical to resolutions of node A from Analysis 1, and are depicted by trees A1, A3, and A4 in Figure 10. The other four, shown in Figure 15, involve placements of the *adducta* group and *odontophora-vincta* group clade that were not supported in Analysis 1. In Analysis 2, the *erigeronis* group and *gigas* are sisters in all trees in which characters have been weighted by the successive approximations procedure.

Tree 1 in Figure 15 is another case in which a hypothetical ancestor is depicted with more than one state for a character, and thus presents the same problems of interpretation discussed for the *bifasciata* group in Analysis 1. Otherwise, there is no strong basis for selecting among the six other resolutions of this node.

It is not surprising that the cladistic relationships among the outgroup taxa in Figure 14 are quite different from Roig-Alsina's (1991) cladogram, since the resolution of outgroup relationships in Analysis 2 is based solely upon characters that were selected because they offered promise of resolving phylogenetic relationships within *Nomada*. A more interesting and significant result of Analysis 2 is that conclusions about the groundplan state for *Nomada* are different for only two of the thirty four characters used in this study, characters 21 and 25. In both cases, optimization on Roig-Alsina's cladogram resulted in an equivocal polarity decision (21-1,3; 25-0,1), whereas Analysis 2 (with characters weighted by successive approximations) decisively chose a single groundplan state (21-3; 25-1). Consequently, the different resolutions of cladistic relationships within *Nomada* in Analysis 2 result more from differences in global parsimony than from conflicting conclusions about character polarity. This can be seen by comparing the weights given to characters by the successive approximations procedure in Analyses 1 and 2 (Table 1). In view of this, the results of Analysis 2 do not provide any strong reason to alter the conclusions from Analysis 1.

After this manuscript had been submitted, the previously unknown male of the South African species *Nomada whiteheadi* was discovered. (Connal Eardley is preparing a detailed description). The male of this species is of special phylogenetic interest because another South African species, *N. gigas*, has a unique combination of male genitalic characters and is the basal lineage of *Nomada* in all of my cladistic analyses. The male genitalia of *N. whiteheadi* do not share any special similarity with those of *N. gigas*, but are similar to those of most other Afrotropical *Nomada* (the *abyssinica* group in the analyses described above, which is incorporated into the *roberjeotiana* species group as explained in the Descriptions of Species Groups). However, the median process of male S8 (character 21) is distinctly longer than wide, resembling the condition in the *vegana* group, and the gonostylus has a sparse basoventral tuft of short, simple setae (character 34). If *N. whiteheadi* is included as a separate terminal taxon in a parsimony analysis, using the hypothetical ancestor of Analysis 1 above as the outgroup and giving all characters equal weight, there are 964 equally parsimonious trees and the strict consensus tree has a basal polytomy of 16 branches (very similar to Figure 13, except that the *vegana* group and *roberjeotiana* group are included in the polytomy rather than being sister taxa). Successive approximations character weighting reduces the number of most parsimonious trees to 108 and places *N. whiteheadi* in a clade with the *vegana* and *roberjeotiana* groups. The same problematic groupings from the analyses described above remain, emphasizing that hypotheses of phylogenetic relationships within *Nomada* are highly sensitive to interpretations of patterns of variation in the male genitalia.

THE QUESTION OF SUBGENERIC CLASSIFICATION OF *NOMADA*

Any comprehensive review of *Nomada* is certain to be at odds with current taxonomic practice for a large part of the genus, because New World workers have tended to recognize subgenera whereas Old World workers have not. Both approaches have their strengths and weaknesses. The International Code of Zoological Nomenclature stipulates (Article 42a) that subgeneric names are to be treated the same, for purposes of nomenclature, as generic names. Using a subgenus as a "dodge" when there are no clear and unequivocal characters to form a basis for defining distinct genera will only generate unnecessary confusion for future workers, because the names will not eliminate the uncertainty about how the taxa should be defined.

Critics of the subgenus concept advocate the use of informal species groups names as a better alternative, because these names have no official nomenclatural status and future workers are not obliged to try to deal with them in resolving nomenclatural problems. However, this has also meant that species group names have been used in an extremely vague manner, and interpreting the names is very difficult, since there is no basis for attributing the names to specimens. At least in *Nomada*, the major reason for confusion about the delineation of "subgenera" or "species groups" is not, in my opinion, a question of whether a particular author chose to use one category or the other to name a given group, but instead whether or not he attempted to specify how the group should be defined. In general, neither school has distinguished itself with outstanding clarity of expression, although there have been occasional notable exceptions on both sides (e.g. Schwarz, 1967, for the *cinctiventris* species group, or Snelling's 1986 subgeneric revision of New World *Nomada*). Neither system is immune to the confusion created by sloppy work.

A different type of dilemma, at least for proponents of a formal cladistic classification, is presented by the branching patterns in the cladograms of Figures 8-10, 14 and 15. A cladistic classification that represented any of these branching patterns would require either a hierarchy of several infrageneric categories within the single genus *Nomada*, or the designation of several genera, some of which would have a few subgenera. Because the branching pattern is not consistently asymmetrical, the convention of phyletic sequencing (Nelson, 1972; summarized and reviewed in chapter 6 of Wiley, 1981) cannot be employed to assign the rank of subgenus to all the infrageneric groups.

In principle, I favor cladistic classifications because the guidelines for erecting such classifications are explicit, and

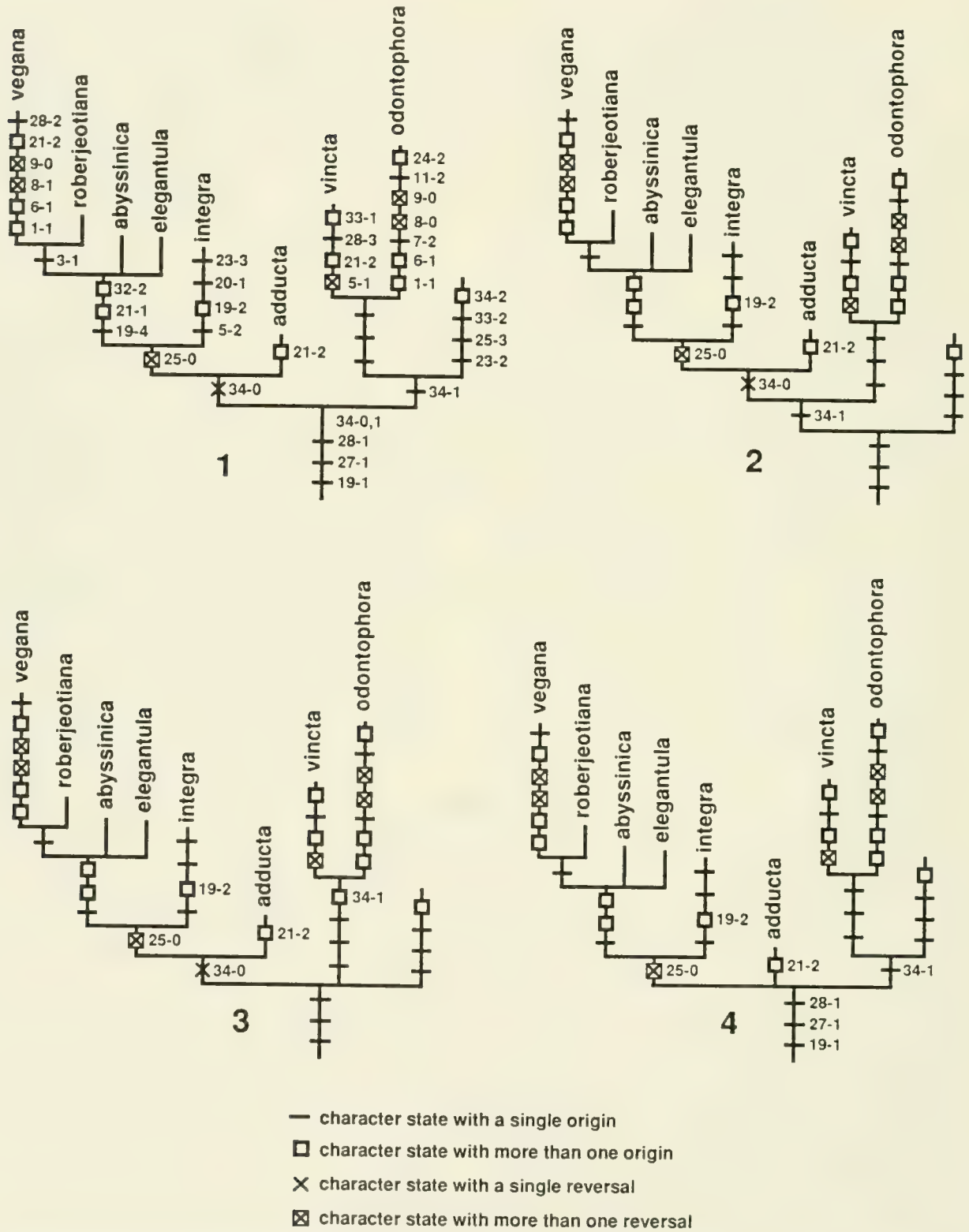


Fig. 15. The four resolutions of polytomy B on Fig. 14 that were not also supported by Analysis 1 (see text for details). Tree 1 shows the distribution of all characters; other trees show only character distributions that differ from tree 1.

the Linnaean hierarchy used in biological classification can unambiguously reflect in a cladistic classification a historical pattern that actually exists in nature, and not merely in the imagination of the classifier. Although I take it as given that there is only one true phylogeny for *Nomada*, it is still far from certain what that phylogeny is. Faced with this uncertainty, and with the rather cumbersome hierarchy that would be required to reflect any of the phylogenetic hypotheses derived from the cladistic analyses, what is the best way to maintain nomenclatural stability while accurately reflecting our current understanding of the phylogeny of this group?

There is considerable evidence, summarized on Figures 8 and 14, to support the hypothesis that the twenty species and species groups treated as the genus *Nomada* in my cladistic analyses constitute a single monophyletic assemblage. Furthermore, this assemblage closely corresponds to the generally accepted concept of the genus *Nomada*. Snelling's (1986) partitioning of New World *Nomada* calls attention to the phenetic distinctness of the groups he elevates to generic rank, *Centrias* and *Hypochrotaenia*. The cladistic analyses presented above indicate that Snelling's *Centrias* and *Hypochrotaenia* are monophyletic, but his *Nomada* is polyphyletic or paraphyletic. If *Nomada* is to be partitioned, I would suggest partitioning it even more than Snelling has, and in such a way as to delineate monophyletic genera.

However, anyone embarking on such an undertaking would encounter a serious problem, given the current chaos in the species-level taxonomy of large parts of the genus. Many species names are presently associated only with female specimens, and the phylogenetic hypotheses presented in this paper depend heavily upon characters of male genitalia, so that it would be necessary to have descriptions of the males of each species in order to confidently place it in the correct genus. Since biological species are, by definition, populations of interbreeding individuals (Mayr, 1942), it is theoretically valid to formulate phylogenetic hypotheses only on the basis of characters of one sex. The other sex is necessarily linked by reproductive ties to the sex upon which the hypothesis is based, and therefore shares its phylogenetic history. However, this theoretical consideration is of limited use to a taxonomist faced with the practical problem of deciding which genus a given species name should be placed in.

Given our current understanding of phylogenetic relationships and of species taxa within *Nomada*, it is my opinion that the worthy goal of a stable and unambiguous nomenclature would be best served by treating *Nomada* as a single, admittedly very large, genus, and by refraining from naming subgenera at least until the species are sufficiently well known that they can be definitely placed in their appropriate groups. Consequently, in this paper I will not be recognizing subgenera, but will instead propose a list of species groups for *Nomada*. In a following section, I will define these groups and provide descriptions. A complete list of species included in each group is being published separately (Alexander and Schwarz, 1994). Although some of the names I will be using can be found in the European literature, the reader should not assume that my use of these names corresponds precisely to that of previous authors (whose concepts are, in most cases, not explicitly stated, but appear to be generally more narrowly defined than mine). For the most part, I will name only groups that are hypothesized to be monophyletic. However, the extent and quality of the evidence for monophyly is quite variable among groups, and the *ruficornis* and *roberjeotiana* groups are paraphyletic. Further comments on the evidence for or against the monophyly of each group are included in the descriptions of species groups.

CHARACTERS EMPLOYED IN DESCRIPTIONS OF SPECIES GROUPS

The following set of characters will be used in describing the species groups of *Nomada* that are recognized in this study. In order to facilitate comparison of descriptions for different species groups, characters will be identified by letter and will be listed in the same sequence in each description. All characters are features of the exoskeleton of adults, and the terminology used here closely follows that of Michener (1944). Characters a to y apply to both sexes, characters A to E apply only to females, and the remaining characters (F - GG) apply only to males. If a character is used in the cladistic analyses, the number assigned to it for those analyses is indicated in parentheses. The abbreviations T and S refer to metasomal terga and sterna, respectively.

(a) **Length/width of labrum**. Usually the labrum is considerably wider than long (L/W < 1, Figures 16, 17), but in a few species it is lengthened until it becomes roughly quadrate or even distinctly longer than wide (L/W > 1, Figure 18).

(b) **Apex of mandible**. There is a tradition among New World systematists dating back to Robertson (1903) of using the presence of a subapical tooth (Figure 21, arrow) on the mandible to define a taxon called the genus or subgenus *Gnathias*. This tooth may be nearly apical as in Figure 21 (the type species of the genus *Nomada*), or more distant from the tip of the mandible, as in most New World species assigned to *Gnathias*. The alternative state is the absence of a subapical tooth (Figures 19, 20, 22).

(c) **Relative length of first two flagellomeres**. (Figures 25 - 29). Because the flagellomeres are asymmetrical, it is necessary to establish a frame of reference for comparing their relative lengths. The established convention is to make the measurement along the shorter side of the first flagellomere (see Figure 26). This character has a long history of use in *Nomada* taxonomy, despite the fact that it varies considerably even within species.

(d) **Preoccipital ridge** may be smoothly rounded, with no trace of a carina or angulation (Figure 30, **pr**), or angulate, or distinctly carinate (Figure 32, **pr**). Although these states are often distinct, intermediates occur.

(e) **Postocciput**. In the *vegana* group, the ventral portion of the postocciput, between the posterior tentorial pits, is distinctly and abruptly recessed below the plane of the postgenal bridge (Figures 30, 31, **po**). In other species groups, the postocciput is nearly on the same plane as the postgenal bridge, with no abrupt, steplike transition between the two regions (Figure 32, **po**).

(f) **Base of proboscideal fossa** (character 1). Usually the base of the fossa is broadly and evenly rounded (Figure 32, **pf**), but in a few groups the hypostomal carina turns inward to form a narrow constriction at the base of the fossa (Figures 30, 31, **pf**).

(g) **Malar space** (character 2). Ordinarily the posterior articu-

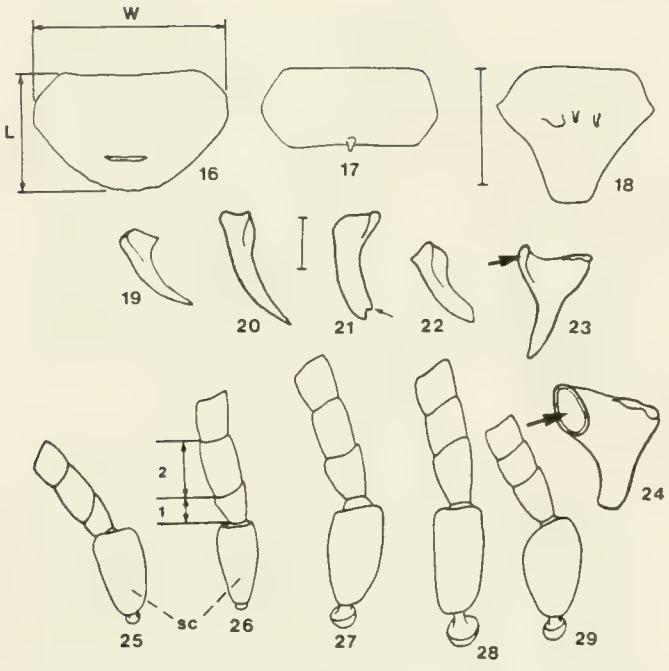


Fig. 16. Labrum of *Nomada articulata*. **L** = length, **W** = width. **Fig. 17.** Labrum of *N. pilipes*. **Fig. 18.** Labrum of *N. panurgina*. **Fig.19.** Right mandible of female *Nomada articulata*, frontal view. **Fig. 20**. Same, *N. panzeri*. **Fig. 21.** Same, *N. ruficornis*. Arrows indicates subapical tooth. **Fig. 22.** Same, *N. striata*. **Fig. 23.** Left mandible of male *Nomada zebrata*, lateral view. Arrow indicates flange near anterior articulation of mandible with head. **Fig. 24.** Same, *N. pilipes*. **Fig. 25.** Scape, pedicel, and first three flagellomeres of antenna of male *N. banksi*, (*ruficornis* group). **Fig. 26.** Same, *N. cressonii*, (*ruficornis* group). Arrows show conventional method of measuring length of first two flagellomeres. **Fig. 27**. Same, *N. luteoloides*,(*ruficornis* group). **Fig. 28.** Same, *N. edwardsii*, (*superba* group). **Fig. 29**. Same, *N. zebrata*, (*vincta* group). Scale bars = 0.5 mm. Figs. 19 - 23, 25 - 29 are all drawn to the same scale; Figs. 16 - 18, 24 are drawn to scale shown by Fig. 18.

lation of the mandible is in contact with or almost touches the ventral margin of the compound eye (Figure 34). In the descriptions, this state will be referred to as "malar space closed posteriorly". In some cases, there is a distinct gap between the base of the mandible and the compound eye, with the gap typically wider in males than in females. Figure 35 illustrates the most extreme development of this state. In the descriptions, this state will be referred to as "malar space open".

(h) **Median portion of pronotal collar** may be evenly rounded, angulate, or sharply carinate, and it may possess a distinct median notch.

(i) **Lateral portion of pronotal collar** may be evenly rounded and subglobose, or rounded when viewed from the front but angulate along the crest of the curve, or distinctly carinate. In addition, the lateral angles may be in the same plane as the rest of the pronotal collar, or they may project anterad.

(j) **Lateral ridge of the pronotum**. In the *vegana* group, there is a distinct ridge on the lateral face of the pronotum (Figures 36, 37, **lr**). This ridge may extend across the neck of the pronotum or it may join the lateral angles of the pronotal collar. In other species groups (e.g. Figure 38), the ridge varies from fairly distinct but rounded to barely discernible or absent altogether.

(k) **Anterior margin of the pronotum** (character 3). When seen in profile, the anterior margin of the pronotum may be distinctly angulate (Figure 36, **ang**), or evenly rounded (Figure 38, **rnd**). Although the distinction is usually fairly clear, intermediates do occur.

(l) **Flange on neck of pronotum**. In the *vegana* group, there is a distinct recurved flange on the anterior rim of the pronotum (Figure 36, **fl**). Nothing like this occurs in other species groups, although a few species of the *roberjeotiana* group have a slightly drawn-up lip on this portion of the pronotum. The distantly related cleptoparasitic genus *Osiris* has an even more pronounced flange than in the *vegana* group.

(m) **Metapleuron** (character 4). Ordinarily the entire exterior surface of the metapleuron is flat or very gently convex, but sometimes it is protuberant dorsally and bears a transverse ridge or lamella (Figure 38, **mtpl**). Snelling (1986) proposed this as an autapomorphy for his genus *Centrias*, although he noted that some species of *Hypochrotaenia* closely resemble *Centrias* in this character.

(n) **Ridge over propodeal spiracle**. The propodeal spiracle may lie flush against the evenly rounded lateral surface of the propodeum (Figure 42), or the spiracle may be recessed, with a ridge directly above it (Figure 38, **pspr**). The distinctness of this ridge may be variable, even within a species.

(o) **Scutellum**. Usually there are distinct dorsal and posterior faces on the scutellum, with a gently rounded or weakly angulate transition between the two faces (Figures 38-40, 43). However, in some cases the scutellum is considerably flattened and more evenly rounded in profile, so that it is difficult to discern a definite posterior face.

(p) **Sculpturing of propodeal enclosure** (character 5). Although the sculpturing of this region varies considerably, a few basic patterns can be discerned. The most common condition (Figures 39, 43) is a coarsely rugose or reticulose region basally (adjacent to the metanotum) and a finely granulose, shagreened, or minutely wrinkled region apically. However, in some groups (*odontophora, adducta, vegana,*and many *roberjeotiana*) the entire surface of the propodeal enclosure is uniformly granulose or shagreened, or bears very fine wrinkles in a whorled pattern suggestive of a fingerprint (Figures 40, 41). In a few cases the surface is smooth and highly polished.

(q) **Lateral margin of propodeal enclosure** is usually marked only by a change in integumental sculpturing, but in many species of the *furva* group it is delineated by a distinct but rather weak carina or ridge (Figure 42, **lr**).

(r) **Procoxal spine** (character 6). The distal portion of the procoxa, mesad of the trochanter, may be produced to form a spinose process (Figures 44 - 47, 178). The shape and conspicuousness of this process vary considerably, even within a species. Often a tuft of setae partially obscures the cuticular spine.

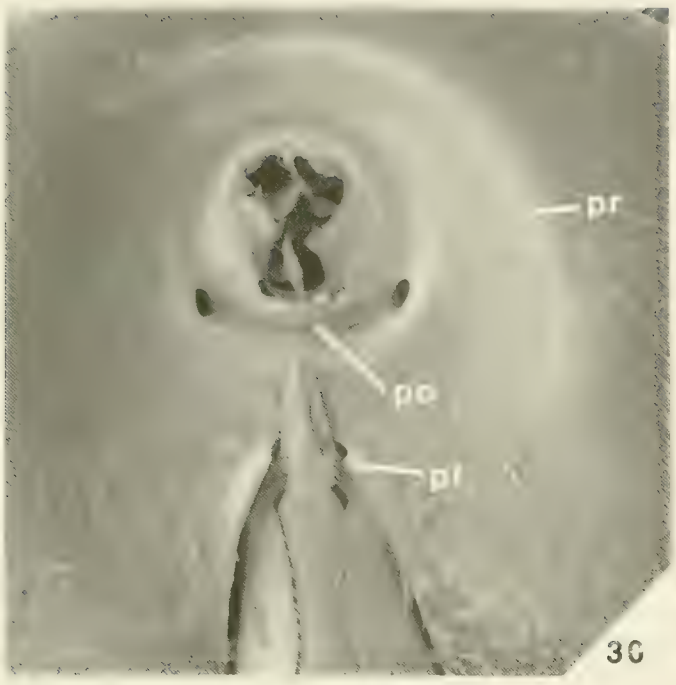
(s) **Lateral carina on procoxa** (character 7). A partial or complete carina may be present on the outer (posterior) face of the procoxa (Figures 6-8 in Snelling, 1986).

(t) **Sculpturing of metasomal terga**. Although there is considerable intergradation, three general patterns may be recognized: (1) punctures distinct, deep, and densely crowded, almost contiguous; (2) punctures weak, indistinct, and more widely spaced (distance between punctures roughly two to five times the diameter of the punctures); (3) punctures absent or extremely minute, inconspicuous, and widely scattered (punctures separated by more than five puncture diameters).

(u) **Apical (posterior) margin of metasomal terga**. Usually integumental sculpturing of type "1" in the preceding character extends almost all the way to the apical margin of the tergum. The alternative condition is a broad apical band, somewhat depressed relative to the base of the tergum, in which punctures are absent or clearly more sparse than in the basal region of the tergum. This latter condition usually, but not always, accompanies sculpturing of type "2" above, and it always (by definition) is found with type "3" sculpturing.

Submarginal cells (Figure 48-50, **smc**). Ordinarily the forewing has three submarginal cells (Figure 50). However, cross veins may be partially or completely lost in two different positions, either of which results in two submarginal cells:

(v) **Vein 1st r-m**. When this vein is absent or incomplete, the



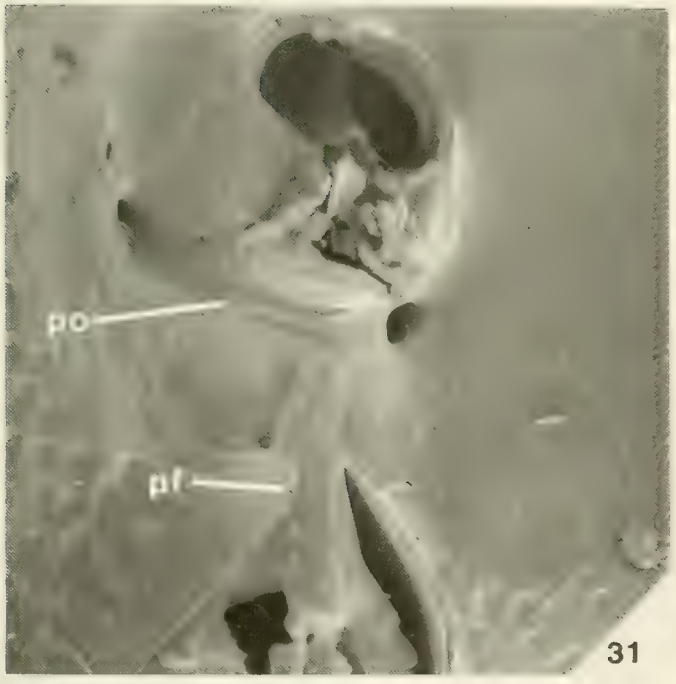


Fig. 30. Back of head of *Nomada pilipes*, (*vegana* group, West Indies), 93X;. **Fig. 31.** Back of head of *N. fervida* (97X), a North American member of the *vegana* group in which the postocciput is only weakly recessed between the posterior tentorial pits. **Fig. 32.** Back of head of *N. imbricata*, (*ruficornis* group), 37X. **Fig. 33.** Top of head of male *N. femoralis*, (*armata* group), 52X; **ff** = oblique facial ridge; **pf** = base of proboscideal fossa; **po** = recessed region of postocciput between posterior tentorial pits; **pr** = preoccipital ridge.

two submarginal cells are roughly equal in length along the posterior margin of the cell (Figure 48). This is the most common type of vein loss that results in two submarginal cells in *Nomada*.

(w) **Vein Rs**. When this vein is absent or incomplete where it would diverge from Rs + M to form the boundary between the first and second submarginal cells, as in Figure 50, the result is a forewing with two submarginal cells that are conspicuously unequal in size, as in Figure 49.

The number of submarginal cells is another character that has been frequently used in *Nomada* taxonomy. However, this is an

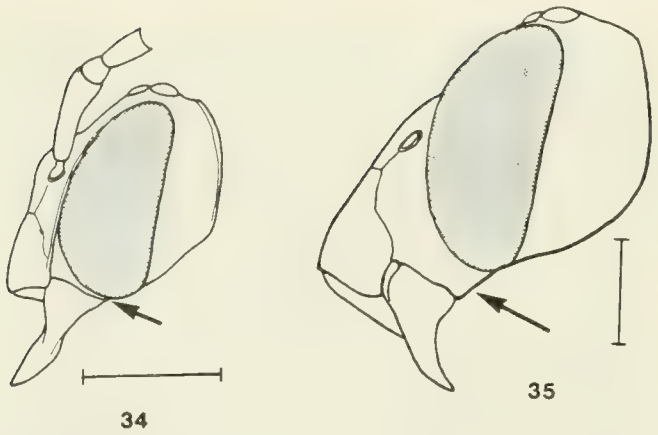


Fig. 34. Lateral view of head of female *Nomada articulata*, (*erigeronis* group). Arrow indicates malar space, which is closed posteriorly. Scale bar = 1 mm. **Fig. 35.** Lateral view of head of male *N. sexfasciata*, (*superba* group). Arrow indicates malar space, which is open posteriorly. Scale bar = 1 mm.

extremely variable character. It is not unusual to find individual specimens with two submarginal cells on one wing and three on the other. Swenk (1913) long ago presented quantitative data on variation of this character in *Nomada obliterata*, a species that usually has two submarginal cells and was proposed as the type species of a new subgenus (*Heminomada* Cockerell and Atkins 1902) solely on the basis of this character. Other taxa that were originally proposed on the basis of having two submarginal cells include *Hypochrotaenia* Holmberg 1886 and *Nomadosoma* Rohwer 1911.

(x) **Apex of marginal cell** (character 8). Usually acute or narrowly rounded and in contact with the costal margin of the forewing (Figures 49, **mca**, 50), but broadly rounded in the *belfragei*, *odontophora* and *vegana* groups (Figure 48, **mca**), and in *rodecki*. Both of these states, as well as additional states not found in *Nomada*, occur in the outgroup.

(y) **Vestiture**. In general, species of *Nomada* have sparse vestiture, as is characteristic of most cleptoparasitic bees. Subtle variations in vestiture have been used in species-level taxonomy, but two states have been employed in defining subgenera. Snelling (1986) emphasized the virtual absence of vestiture on the propodeum in New World *Nomadita*, and Broemeling (1988) used a vestiture of "densely appressed hair (completely hiding the integument beneath)" as a diagnostic trait for his new subgenus *Asteronomada*.

THE NEXT FIVE CHARACTERS PERTAIN ONLY TO FEMALES.

(A) **Paraocular ridge** (character 9). The narrow region between the apicolateral angle of the clypeus and the lower, inner margin of the compound eye may be evenly convex (Figure 51, arrow) or it may be crossed by a distinct carina or at least a sharp angulation referred to as the paraocular ridge (Figure 52, arrow). This ridge may or may not extend upward along the inner margin of the compound eye as a distinct carina, but coding of its presence or absence in the species group descriptions will refer only to the region between the apicolateral angle of the clypeus and the lower margin of the compound eye.

(B) **Spinose setae on outer (anterior) face of hind tibia**. Although distinct tubercles bearing short, thornlike setae are often present on the hind tibiae of female *Nomada*, only in the *odontophora* group (Figure 21 in Schwarz, 1966) and some species of the *vegana* group (Figures 9, 10 in Snelling, 1986) do females have very large, robust, conspicuously spinose setae on the outer face of the hind (and often the middle) tibia. Similar spinose setae occur in some other genera of the Nomadinae as well.

(C) **T5**. As described earlier, the apical margin of this tergum always has a patch of specially modified setae comprising the *pseudopygidium* or *prepygidial fimbria* (Figure 6). Usually this is a fairly narrow, transverse band of flattened, reflective setae, often appearing silvery or white when viewed with an optical microscope, or squamous when viewed with a scanning electron microscope (Figure 6). A few distinctive modifications of this condition that are readily visible with an optical microscope will be described under the appropriate species groups.

(D) **Pygidial plate** usually tapers from the base to a narrowly rounded apex (Figures 5, 59, **ppl**, Figure 6, **pyg**), but in some species in the *vegana*, *trispinosa*, *basalis*, and *superba* groups, the apex is more broadly rounded and the sides are more or less parallel (Figure 60, **ppl**).

(E) **Distal setae of hind tibia** (character 15). The apex of the hind tibia almost always bears at least a few specialized setae that are distinct from those on the rest of the tibia. These setae vary in subtle ways that are often useful in species-level taxonomy. However, a few species groups can be characterized by shared apomorphic states of this character. The plesiomorphic state for *Nomada* is hypothesized to be a small number (roughly ten or fewer) of stiff, spinose setae that are often distinctly melanized (Figure 53). Apomorphic states useful for delineating species groups or subgroups are the following, numbered as in the cladistic analyses: (2) setae very stout, short, apically blunt, generally peglike in overall appearance (Figure 55, *trispinosa* group); (3) apex of hind tibia with a flattened area bearing a dense cluster of stout, straight, flattened setae (Figure 54, *armata* group); (4) setae relatively long and narrow, not heavily melanized, in a dense cluster of about 10 to 25 setae (Figures 56, 57, *superba* and *basalis* groups); (5) setae broad, flat, bladelike, apically curved, often partially overlapping one another (Figure 58, *bifasciata* group).

THE FOLLOWING CHARACTERS APPLY ONLY TO MALES.

(F) **Anterior articulation of mandible**. Often there is a distinct recurved flange along the anterior base of the mandible, where it contacts the apicolateral corner of the clypeus (Figure 23, arrow). Sometimes the flange is so large and so strongly recurved that it resembles a flattened disc or platform (Figure 24, arrow).

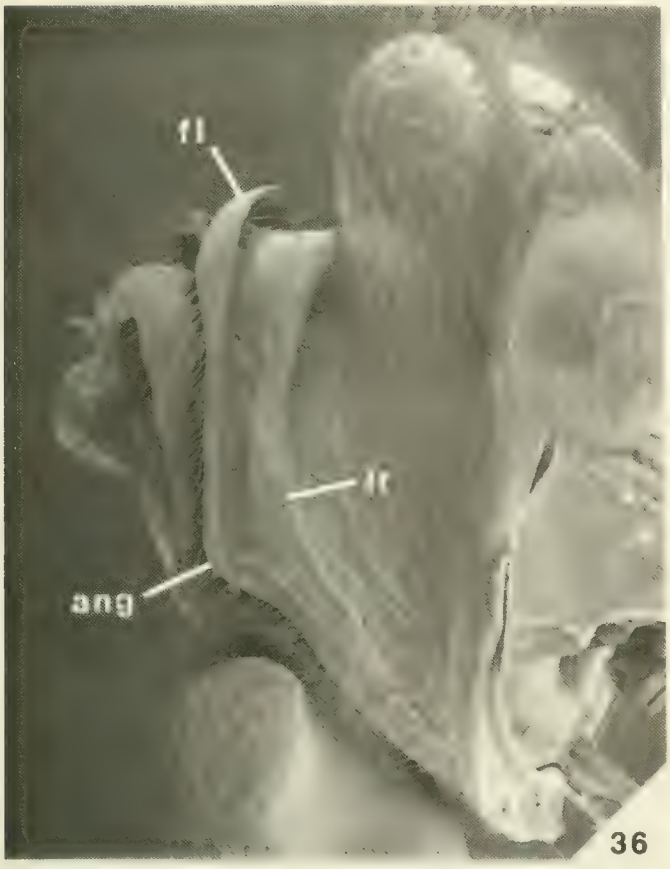
(G) **Scape** (character 16). The shape and diameter of the scape varies considerably, from a cylinder about the same diameter as the flagellum (Figure 26, **sc**), to a cylindrical structure roughly twice the diameter of the flagellum and completely enclosing the pedicel (Figure 25, **sc**), to a conspicuously swollen, subglobose structure (Figure 29).

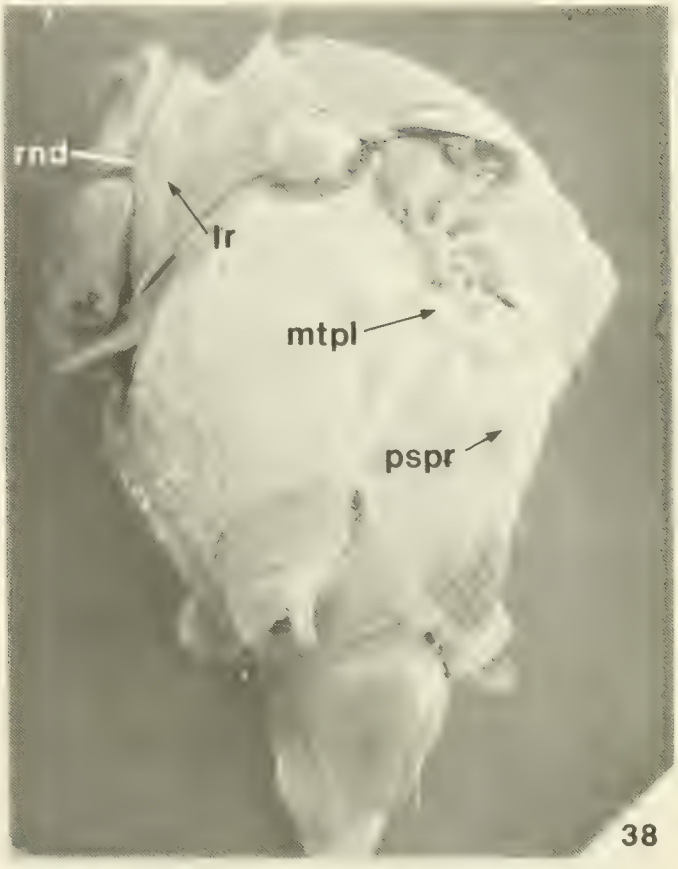
(H) **Oblique frontal ridge** (character 17). Species in the Old World *armata* group have distinctive oblong ridges on the face adjacent to the upper, inner margins of the compound eyes (Figure 33, **ff**). The integument has a granulose or porous appearance within these oblong areas. Schwarz uses the terms Augenplatten (e.g. Schwarz, 1974, 1977) or Stirnplatten (e.g. Schwarz, 1987) for these structures.

(I) **Protarsal brush**. Often the front tarsi have long, brushlike setae arising from the inner, apical portions of the tarsomeres (Figure 61, **ptb**, also Figures 3, 10 in Eardley & Schwarz, 1991). Various degrees of reduction occur, and in some species no distinct brush can be discerned.

(J) **Front femur**. Although usually roughly cylindrical and similar in shape to the middle and hind femora, the front femur is occasionally greatly enlarged in a variety of ways. The only New World species with such modified front femora, *hesperia* (Figure 62, **fm**), has been placed in a monotypic subgenus, *Laminomada* (Rodeck, 1947), but several Old World species have variously modified front femora (Figures 63-64, **fm**).

(K) **Base of hind femur** (character 18). The base of the hind femur may be broadly excavated ventrally and may bear a dense tuft, or flocculus, of long, plumose setae (Figure 67, **fl**). Intermediates exist between a very distinct, conspicuous flocculus and a weak, indistinct one. In the *bifasciata* group, both the trochanter and the femur have specially modified setae, those on the femur being strongly appressed and resembling a patch of felt when viewed under an optical microscope. With scanning electron microscopy, it can be seen that the femoral setae are broadened and





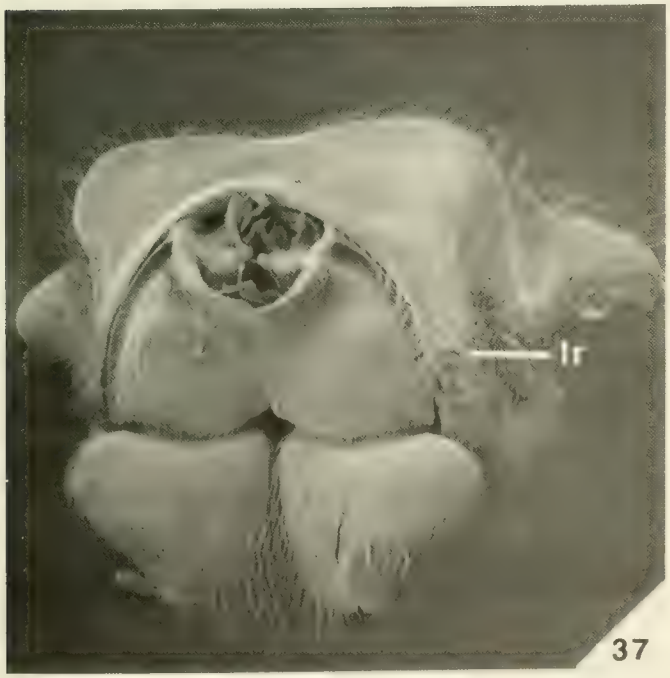
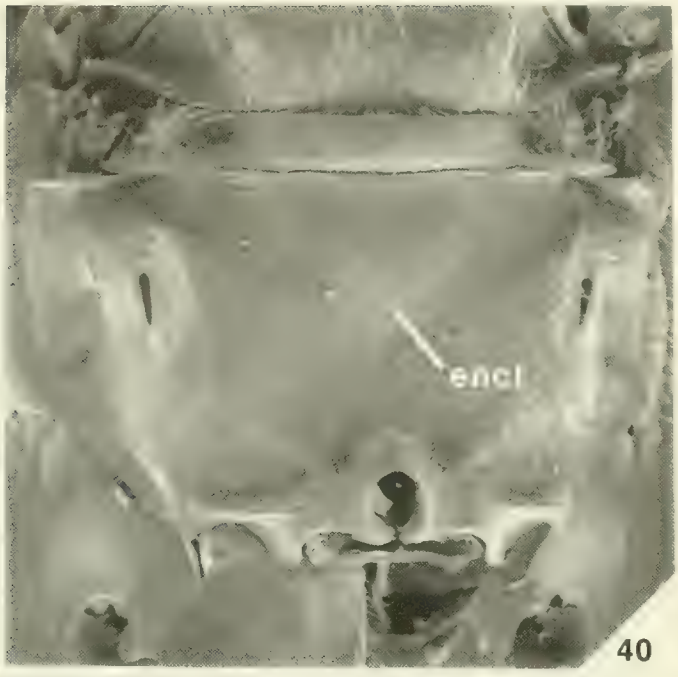


Fig. 36. Lateral view of pronotum of *Nomada krugi*, (*vegana* group), 100X; **Fig. 37.** Oblique frontal view of pronotum of *N. pilipes*, (*vegana* group), 58X; **Fig. 38.** Lateral view of mesosoma of *Nomada articulata*, (*erigeronis* group), 68x. **Fig. 39.** Oblique dorsal view of posterior face of mesosoma of *N. integra*, (*integra* group); **ang** = angulate anterior margin; **encl** = propodeal enclosure; **fl** = distinct flange on neck of pronotum; **lr** = lateral ridge; **mtpl** = protuberant upper area of metapleuron; **pspr** = ridge above propodeal spiracle; **rnd** = rounded anterior margin of pronotum.



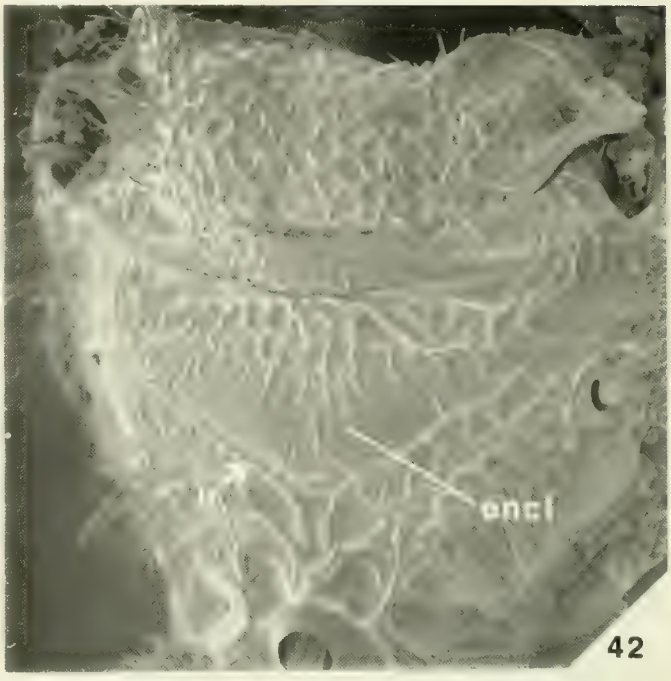


Fig. 40. Posterior view of mesosoma of *Nomada pilipes*, (*vegana* group), 55X; **Fig. 41.** Same, 97X, showing sculpturing of propodeal enclosure; **Fig. 42.** Oblique posterior view of mesosoma of *Nomada furvoides*, (*furva* group), 104X; **Fig. 43.** Oblique posterior view of mesosoma of *N. imbricata*, (*rufiventris* group) 49X; **encl** = propodeal enclosure; **lr** = ridge marking lateral margin of propodeal enclosure.

flattened basally (Figure 68). In the *trispinosa* group, the ventral face of the hind femur has long, erect, plumose setae arranged in distinct anterior and posterior rows (Figure 65). The structure is somewhat reminescent of the scopa of many nest-provisioning female bees, except that the rows of setae never extend more than half the length of the femur and the setae are rather sparse.

(L) **Subgenital brush** (character 19). S6 bears an apical tuft of setae, the *subgenital brush* (Snelling, 1986), whose form varies considerably. Snelling proposed a dichotomy, "simple" and "complex", but I have not found this adequate to describe the variety of forms of the brush, especially when Old World taxa are considered. For the cladistic analyses, I recognized the following

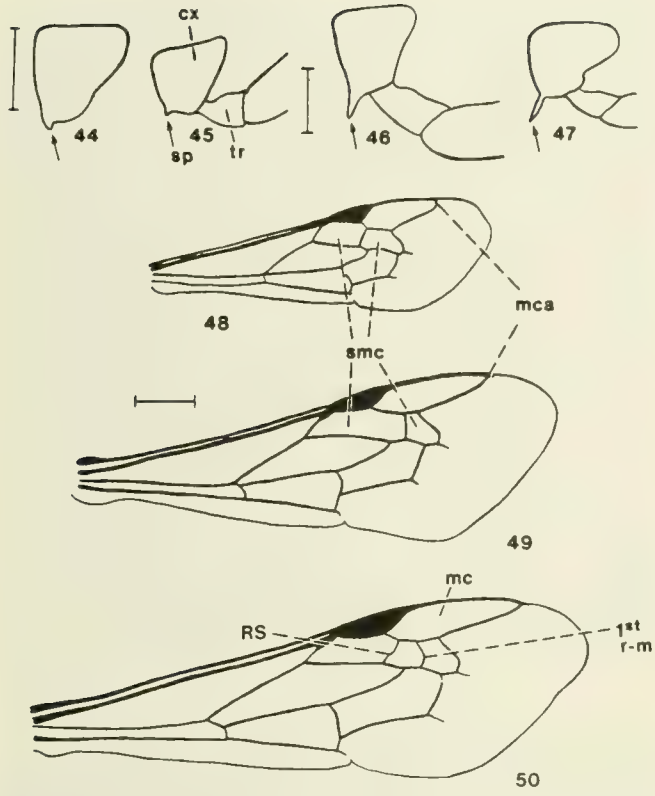


Fig. 44. Procoxa of *Nomada banksi*, (*ruficornis* group), frontal view. Arrow indicates spinose process. Scale bar = 0.5 mm for Figs. 44 - 47; **Fig. 45**. Same, *N. articulata*, (*erigeronis* group); **Fig. 46.** Same, *N. rubicunda*, (*erigeronis* group); **Fig. 47.** Same, *N. vegana*, (*vegana* group); **Fig. 48.** Right front wing of *N. pilipes* (*vegana* group); Scale bar = 1 mm. for Figs. 48 - 50; **Fig. 49**. Same, *N. obliterata*, (*ruficornis* group); **Fig. 50.** Same, *N. imbricata*, (*ruficornis* group); **cx** = coxa; **mca** = apex of marginal cell; **mc** = marginal cell; **1st r-m** = vein 1st r-m; **RS** = 3rd abscissa of vein Rs; **smc** = submarginal cell; **sp** = spinose process; **tr** = trochanter.

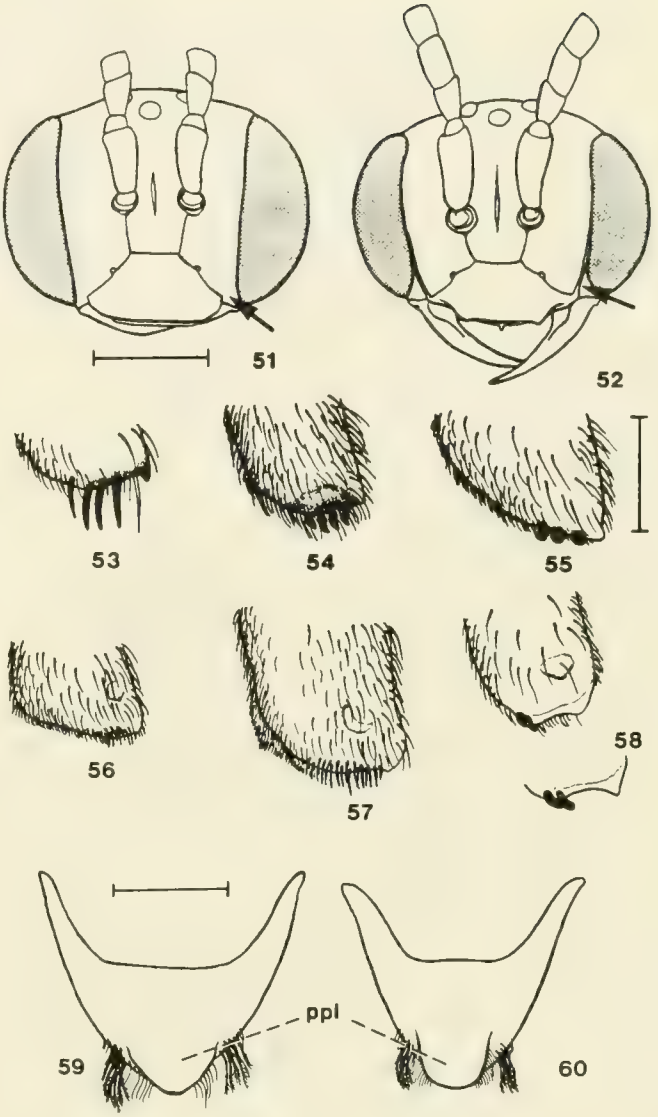


Fig. 51. Head of female *Nomada vegana*, (*vegana* group), frontal view. Arrow indicates position of paraocular ridge, which is absent in the *vegana* group. Scale bar = 1 mm. **Fig. 52.** Head of female *N. banksi*, (*ruficornis* group), frontal view. Arrow indicates paraocular ridge. Same scale as Fig. 51. Figs. 53 - 55, 58 drawn to same scale, with scale bar (by Fig. 55) indicating 0.25 mm. The same scale bar indicates 0.5 mm for Figs. 56 and 57. **Fig. 53.** Apex of hind tibia of female *Nomada banksi*, (*ruficornis* group); **Fig. 54**. Same, *N. panurgina*, (*armata* group); **Fig. 55.** Same, *N. trispinosa*, (*trispinosa* group); **Fig. 56**. Same, *N. sexfasciata*, (*superba* group); **Fig. 57.** Same, *N. grandis*, (*superba* group); **Fig. 58.** Same, *N. luteoloides*, (*ruficornis* group). Two individuals are shown in (a) and (b). Species in the *bifasciata* group also have the same type of specialized hindtibial setae. **Fig. 59.** Female tergum 6, dorsal view, *N. vicina*, (*ruficornis* group); **Fig. 60.** Same, *N. superba*, (*superba* group). Freehand sketch. **ppl** = pygidial plate. Scale bar = 0.5 mm.

seven states: (0) absent; (1) setae short, recumbent laterally, suberect mesally, brush inconspicuous (Figure 7a); (2) setae longer, brush more conspicuous, with a median tuft of erect or suberect setae and lateral tufts of recumbent, laterally directed setae (Figure 7b); (3) median tuft absent or extremely weak, lateral tufts very dense and conspicuous (Figure 7g); (4) setae long, erect, often recurved apically, relatively sparse and confined to median portion of apex of S6 (or occasionally extending logitudinally down the centers of S4 and S5, Figures 7c,d); (5) setae extremely long, erect, apically plumose, in some cases forming two or three distinct tufts (Figures 7e,f, 69); (6) setae long, plumose, confined to apical margin of sternum 6 and horizontally directed, not erect as in states 4 and 5, not interrupted mesally as in state 3 (Figure 7h).

(M) **Apex of S6**. In most cases the apical margin is at least moderately produced medially (e.g. Figures 7a,b,c,d,g), but in species of the *erigeronis* group with a very elaborate, three-tufted subgenital brush, the apical margin of the sternum is not produced, but more or less truncate (Figure 7f). In the *bifasciata* group, the apical margin is more conspicuously produced and narrower than in other species groups (Figure 7h).

(N) **Setal fringe on male metasomal sterna** (character 30). Although there are always at least a few simple setae on the metasomal sterna, in a few groups some or all of the sterna of metasomal segments 2-5 have setae that are conspicuously lengthened and densely packed to form a distinct subapical fringe (Figure 7e). In most species of the *erigeronis* group, the

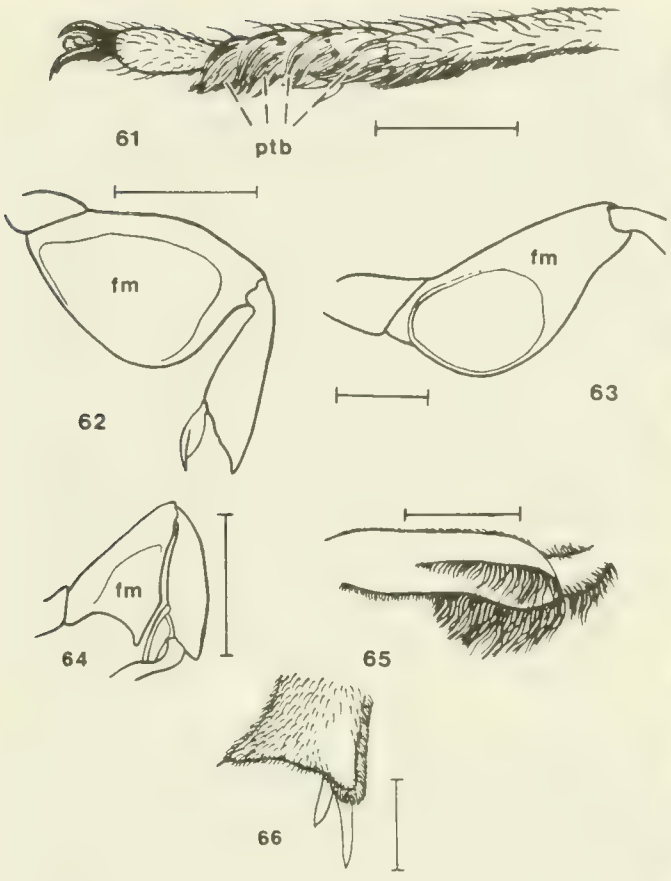


Fig. 61. Front tarsus of male *Nomada vegana*, (*vegana* group); **Fig. 62.** Left front leg, anterior view, male *N. hespera* (*behrii* group); **Fig. 63.** Same, male *N. sanguinea*, (*armata* group); **Fig. 64.** Same, male *N. femoralis*, (*armata* group); **Fig. 65.** Oblique ventral view of hind femur of male *N. trispinosa* (*trispinosa* group); **Fig. 66.** Apex of hind tibia of male *N. armata* (*armata* group), posterior view; **fm** = femur; **ptb** = protarsal brush; scale bar = 0.5 mm for Figs. 61, 63, 65, 68; = 1 mm for Figs. 62, 64.

setae are very densely packed, but recumbent rather than erect (Figures 7f, 69).

(O) **Pygidial plate**. A frequently mentioned character, especially in identification keys, is the presence or absence of an apical notch on the pygidial plate (Figures 70-72). Often the distinction is clear and unequivocal, but there are cases (e.g. Figure 71) in which the notch is only a very shallow emargination. In such cases, a species may have some individuals that have a notched pygidial plate and others that do not.

(P) **S7** (character 20). The range of variation in the shape of this sclerite defies simple categorization (see Figures 73 - 75, 153, 156, 169, 170 for a few examples). In the *integra* group, the shape of S7 is both distinctive and reasonably consistent. The lateral arms are relatively long and narrow, and the median process is roughly parallel-sided, narrow, and apically truncate or weakly concave (Figures 107 - 109). Schwarz (1967) described this shape as "reminding one of a horseshoe". This unique state is postulated to be autapomorphic for the *integra* group. The state found in the South African species *gigas* is also unique (Figures 100, 101). There are also individual species or groups of closely related species, as within the *armata* group, that have distinctive and undoubtedly apomorphic modifications of S7.

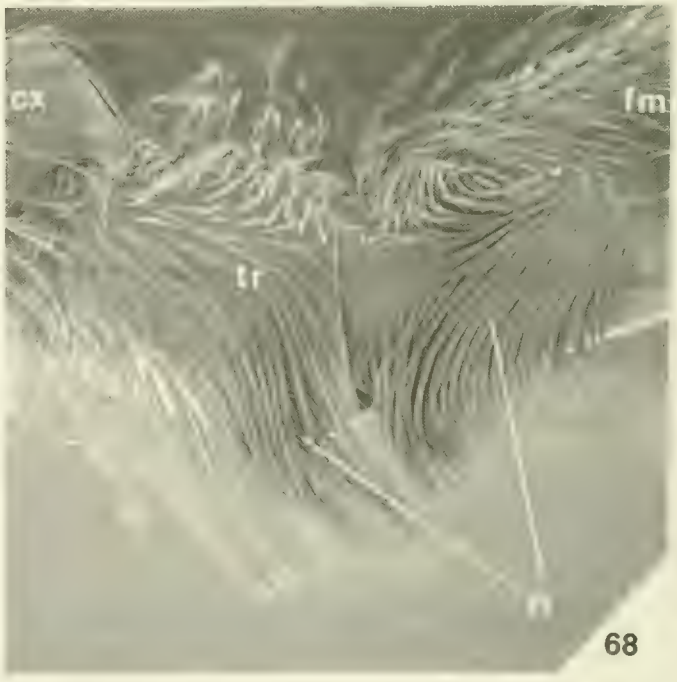


Fig. 67. Hind trochanter and femur of male *Nomada femoralis* (*armata* group), 182X; **Fig. 68.** Base of hind leg of *N. bifasciata*, (*bifasciata* group), 88X; **cx** = coxa; **fl** = flocculus; **fm** = femur; **tr** = trochanter.

(Q) The existence **on S8** of a conspicuous **median apical process** bearing spinose setae (character 21) is autapomorphic for the genus *Nomada*. However, the shape of this median process is quite variable. The forms of this structure within *Nomada* are: (1) proc-

69

Fig. 69. Ventral view of metasoma of male *Nomada articulata* (*erigeronis* group), 40X; **br** = subgenital brush; **fr** = setal fringe (cf. Figs. 7e,f).

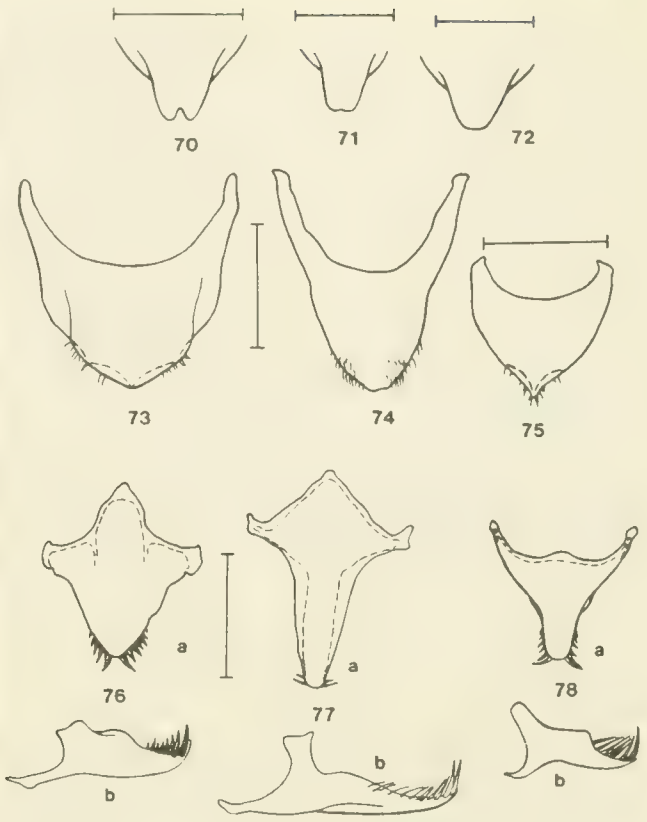


Fig. 70. Pygidial plate, male *Nomada articulata*, (*erigeronis* group); **Fig. 71.** Same, *N. trispinosa*, (*trispinosa* group); **Fig. 72.** Same, *N. basalis* (*basalis* group); **Fig. 73.** Male metasomal sternum 7, *N. basalis*.; **Fig. 74.** Same, *N. zebrata*, (*vincta* group); **Fig. 75.** Same, *N. distinguenda*, (*furva* group); **Fig. 76.** Male metasomal sternum 8, *N. crotchii* (*erigeronis* group); (a) ventral view; (b) lateral view; **Fig. 77.** Same, *N. zebrata* (*vincta* group); (a) ventral view; (b) lateral view; **Fig. 78.** Same, *N. vegana* (*vegana* group); (a) ventral view; (b) lateral view. Scale bar = 0.25 mm for Fig.75; = 0.5 mm for Figs. 72-74, 76-78; = 1 mm for Figs. 70, 71.

ess dorsoventrally compressed, short, and broad (length roughly equal to width), tapering from the base to a broadly rounded apex (Figure 76); (2) process dorsoventrally compressed, but distinctly longer than broad, tapering to a narrowly rounded apex (Figures 77, 78); (3) process laterally compressed, long and narrow (always much longer than wide, although the width is variable), frequently somewhat expanded apically (Figures 80 - 83); (4) laterally compressed as in state 3, but much shorter (length roughly equal to width in ventral view), distinctly expanded apically (Figure 79).

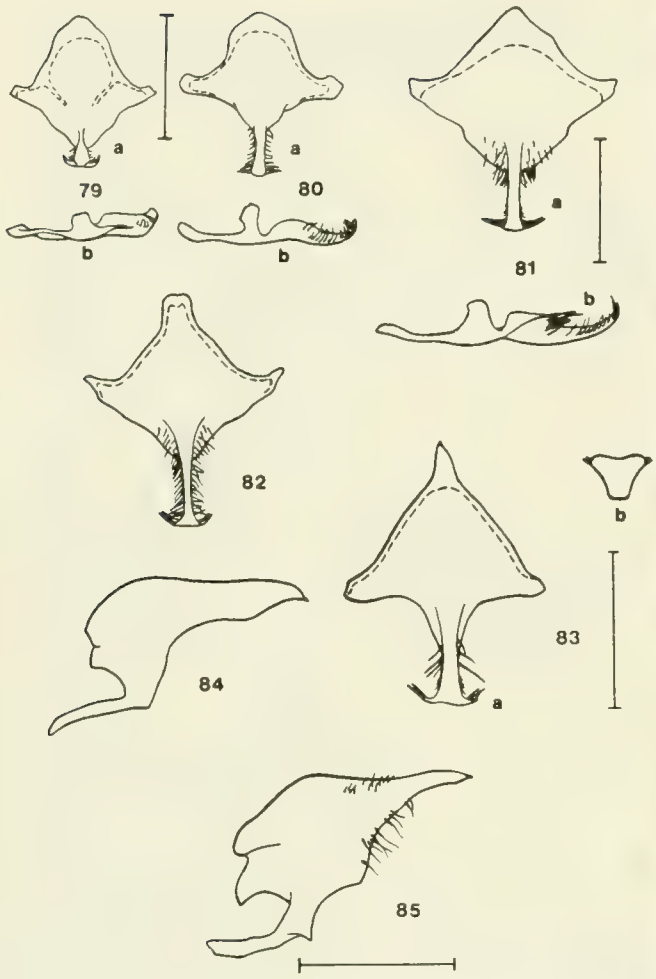
(R) **Lateral profile of S8**. The median process may lie in roughly the same plane as the basal portion of the sternum (Figures 77b, 79b-81b), or it may lie at a distinct angle to the plane of the basal portion of the sternum (Figure 78b). Occasional intermediates occur (e.g. Figure 76b).

(S) **Spinose setae on median process of S8** (character 22). As mentioned above, at least a few relatively stiff, stout, spinose setae are almost always present. Very often the most distal setae are the most robust. In the *erigeronis*, *vegana*, and *roberjeotiana* groups, these spinose setae are very robust and clawlike (as in Figure 76).

(T) **Shape of gonostylus** (character 23). This is another highly variable, complex character that cannot easily be coded into discrete states. Snelling's (1986) basic subdivision into gonostyli that are short, stout, and bluntly rounded apically (e.g. Figures 86, 88-91) versus those that are longer, more slender, and more narrowly rounded apically (e.g. Figures 87, 117, 121-123, 136-141) works reasonably well for most New World species. However, Old World groups exhibit a variety of forms that cannot be accommodated within a simple dichotomy. In the *integra* group, considerable variability exists at the species level (e.g. Figures 112, 116, also see figures in Schwarz, 1967), and nothing within the spectrum of variability bears much resemblance to what occurs in other groups. The *furva* and *trispinosa* groups have long, narrow, cylindrical gonostyli, but they are always very distinctly curved toward the midline of the genital capsule (Figures 172, 173). The *bifasciata* group is similar, but the gonostyli are more flattened in cross section, and in some species the apex is strongly modified (Figures 166-168). A few Old World species, such as *basalis* and *nobilis*, also have unusual modifications of the gonostylus (Figures 149-152). In the *odontophora* group, there is a distinct transverse ridge dorsally at the base of the long, narrow, cylindrical gonostylus (Figure 128).

(U) **Inner basal shelf on gonostylus** (character 24). A small but distinct shelflike projection on the inner base of the gonostylus is often present (Figures 90, 91). It may or may not bear a cluster of specially modified setae that are short, stout, and heavily melanized. Snelling (1986) refers to these setae as the "inner, basal setal cluster".

(V) **Vestiture of gonostylus** (character 25). As with the shape of the gonostylus, its vestiture varies considerably. The inferred plesiomorphic condition consists either of relatively sparse, simple



Figs. 79-83. Male metasomal sternum 8: **Fig. 79.** *Nomada distinguenda*, (*furva* group); (a) ventral view; (b) lateral view; **Fig. 80.** *N. banksi*, (*ruficornis* group); (a) ventral view; (b) lateral view; **Fig. 81.** *N. edwardsii*, (*superba* group); (a) ventral; (b) lateral; **Fig. 82.** *N. nobilis*, (*basalis* group); **Fig. 83.** *N. trispinosa* (*trispinosa* group); (a) ventral view; (b) apex of median process, viewed looking down its longitudinal axis; **Fig. 84.** Outline of penis valve of *N. trispinosa*, lateral view; **Fig. 85.** Lateral view of penis valve of *N. bifasciata*, (*bifasciata* group). Scale bar = 0.25 mm for Fig. 79; = 0.5 mm for Figs. 80-85.

setae, some of which are greater than half the length of the gonostylus (e.g. Figures 98, 130, 132, 133, 136-139), or sparse, simple setae that are less than or equal to half the length of the gonostylus (e.g. Figures 87, 117, 121, 127). States that occur only within *Nomada* and are thus inferred to be apomorphic are: (i) setae at least as long as gonostylus and very dense, weakly plumose or sinuate apically (e.g. Figures 86, 88-91); ii) setae as in the preceding, but distinctly separated into basal and apical fields, with the apical tufts generally shorter and denser than the basal field (Figures 172-174); (iii) as in the preceding, but the apical tuft distinctly subdivided (Figure 157, 158, 166-168).

(W) **Basoventral lobe of gonostylus** (character 33). The ventral base of the gonostylus may bear a distinct lobelike structure. Although the range of variation is considerable and fairly continuous, two general types of lobe can be distinguished: (1) lobe circular in cross section, more or less hemispherical or digitiform (e.g. Figures 86, 90, 91, 150, 154); (2) lobe not circular in cross section, but forming a transverse ridge (e.g. Figures 161, 166, 173).

Fig. 86. Lateral view of gonostylus of *Nomada banksi*, (*ruficornis* group), 188X; **Fig. 87.** Same, *N. utahensis*, (*vincta* group), 145X.

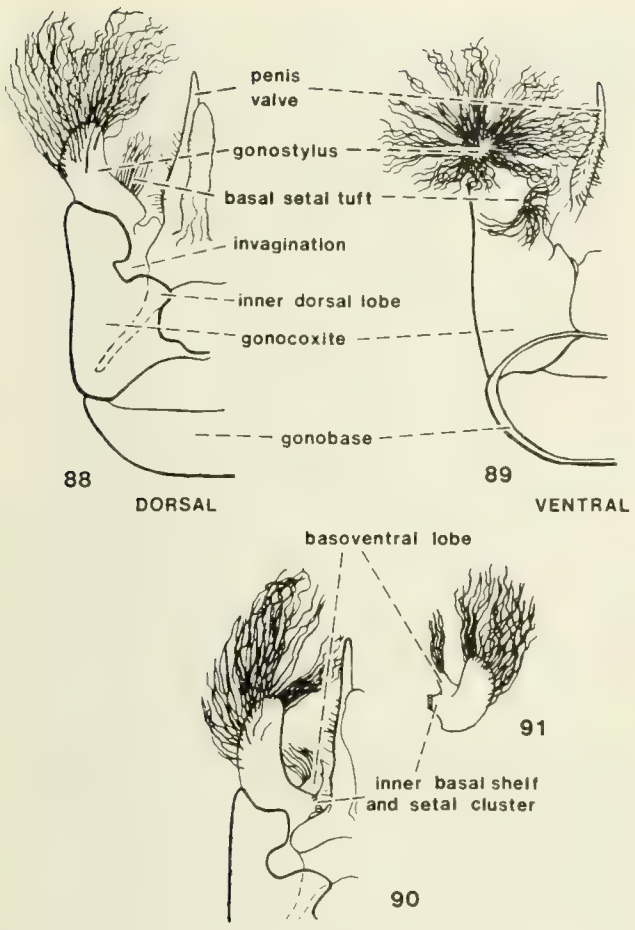


Fig. 88. Genital capsule of *Nomada banksi* (*ruficornis* group), dorsal view; **Fig. 89.** Same, ventral view; **Fig. 90.** Genital capsule of *N. luteoloides*, (*ruficornis* group), dorsal view. **Fig. 91.** Gonostylus of *N. luteoloides*, viewed looking down longitudinal axis of genital capsule.

(X) **Setal tuft at base of gonostylus** (character 34). In species that have the basoventral lobe on the gonostylus, there is also a distinct cluster of setae arising from the lobe. In the *adducta* and *odontophora* groups, the setae are short and simple (Figures 87, 122, 127). In the other subgenera with a basoventral tuft of setae, the setae are very long (at least half as long as the gonostylus) and often plumose or sinuate apically (e.g. Figures 86, 89-91). Such a tuft of setae is not necessarily associated with a basoventral lobe on the gonostylus (e.g. Figures 146, 148). In other words, the setal tuft may occur without the lobe (although it is more likely to consist of only a few setae in such cases), but if there is a lobe there is always a setal tuft.

(Y) **Gonobase** (**Basal ring of genital capsule**). The plesiomorphic condition is a ring about the same diameter as the joined bases of the gonocoxites, projecting beyond the bases of the gonocoxites in lateral view (e.g. Figures 88, 98, 112, 117, 121, 128). In the *vegana* group, the gonobase is greatly reduced, less than the width of the joined bases of the gonocoxites and not projecting beyond the bases of the gonocoxites in lateral view (Figures 133-135). Considerable reduction of the gonobase is also consistently found in the *roberjeotiana* group (Figures 130, 136-138), and a BMNH specimen identified as the Ethiopian species *hararensis* Meade-Waldo has the gonobase as reduced as in the *vegana* group (Figures 140, 141).

(Z) **Ventral hook on penis valves** (character 26). A distinctive short, sharp, toothlike process (or "hook") on the ventral margin of the penis valves (indicated by the arrow on Figures 122, 123, and 127, also visible in Figure 93, **vh**) occurs in all species of the *adducta* and *odontophora* groups. Snelling (1986, p.23) refers to this structure as "male aedeagus with a ventral hook".

(AA) **Inner ridge on penis valve** (character 31). On the inner face of the penis valves, just above the point where the membranous aedeagus, or penis, joins with the valves, a small but distinct ridge occurs in the *adducta* and *odontophora* groups (indicated by the arrows in Figures 124-126 and 129, **ir** in Figure 93). More detailed comments on the variation in this character are included in the descriptions of those species groups.

(BB) **Outer lateral ridge on penis valve** (character 32). In most *Nomada*, the outer face of the penis valves is distinctly flattened, and the valve (above the apodemes) is more or less planar in cross section (see Figure 96). However, three modifications of this shape can be discerned: (1) the *vincta* and *odontophora* groups have a rounded or weakly angulate, rather weltlike lateral ridge (Figures 93 **or**, 124-126, 129); (2) the *erigeronis*, *vegana* and *roberjeotiana* groups have a sharp, distinctly carinate lateral ridge, and the penis valve is roughly triangular in cross section (Figures 92, 94, 95, **or**); (3) *Nomada gigas* has a unique feature that can perhaps best be described as a sinuous furrow marked by a distinct ridge on its outer edge (Figures 98, 99).

(CC) **Penis valve dorsally flattened** (Figures 92, 133, 135). This condition occurs only in the *vegana* group, although it may represent a further modification of the basic form of the penis valve that is characteristic of the *erigeronis* and *roberjeotiana* species groups.

(DD) **Basoventral swelling on penis valve**. Although varying in prominence, a swelling on the ventral surface of the penis valves, at approximately the level where the gonostyli articulate with the gonocoxites (Figure 173, **sw**), is discernible in species of the *furva* group. Even in species where this region of the penis valves does not appear strongly swollen, one can discern a weak concavity on the outer face of the penis valves adjacent to the inner basal shelf on the gonostylus. There appears to be a close fit between this shelf on the gonostylus and the adjacent face of the penis valve, and perhaps the distinctive swollen area on a species such as *distinguenda* (Figure 173) could function to improve the efficiency of some kind of grasping or locking mechanism involving the gonostylus and penis valve.

(EE) **Apex of penis valve** is usually acute or narrowly rounded, both in *Nomada* and in the outgroup (e.g. Figures 92-96), so this is inferred to be the plesiomorphic condition. In the *integra* group, the apex is never like this, although it exhibits a variety of derived states. The groundplan state for the *integra* group is probably a rounded, slightly bulbous apex (Figure 97), which is further modified to form pincerlike structures in species like *beaumonti* (Figure 114) and *carthaginensis* (Figure 131 in Schwarz, 1967, also see his Figures 26, 42, and 65).

(FF) **Invagination of dorsal gonocoxite** (character 27). The posterior margin of the gonocoxite often bears a conspicuous invagination, although its shape and orientation vary considerably (e.g. Figures 88, 90, 110, 113, 115, 117, 121, 133, 138).

(GG) **Inner dorsal lobe of gonocoxite** (character 28). Because the gonocoxites do not meet along the dorsal midline of the genital capsule, they are separated by a gap that Snelling (1986, p. 5) termed the median sinus. When there is a distinct invagination on the dorsal gonocoxite, there will also be a dorsal lobe (Snelling, 1986) between this invagination and the median sinus (Figure 88). Most often this dorsal lobe is about as long as broad, and gently rounded apically (e.g. Figures 88, 90). In the *vegana* group, it tends to be much longer than broad, giving it an appearance that Snelling aptly described as digitiform (Figure 133). In the *vincta* group, the dorsal lobe is rather indistinct, and Snelling has interpreted this as a consequence of the lobe being much broader than long, with the median sinus between the gonocoxites reduced to a narrow slit (Figure 121). Clearly the median sinus, invagination of the gonocoxite, and inner dorsal lobe of the gonocoxite are interrelated, and the most appropriate interpre-

Figs. 92-95. Penis valves: **Fig. 92.** *Nomada pilipes*, (*vegana* group), 260X, ventral view; **Fig. 93**. Left valve of *N. utahensis*, (*vincta* group), 208X, viewed looking down longitudinal axis of genital capsule; **Fig. 94.** Right valve of *Nomada articulata*, (*erigeronis* group), oblique lateral view; **Fig. 95**. *N. placida*, (*roberjotiana* group), 220X; tip of left valve is broken off; **ir** = ridge on inner face of penis valve; **or** = ridge on outer face of penis valve; **vh** = ventral hook.

tation of homologous states is problematic. For the purposes of the cladistic analysis, the invagination was interpreted as a single character state that was either present or absent, and the dorsal lobe seemed distinct enough in the *vegana* and *vincta* groups to warrant coding it as autapomorphic for each taxon. Under this interpretation, inferred derived states merely provided additional evidence corroborating the monophyly of groups whose monophyly is also supported by other, independent characters.

Fig. 96. Penis valves of *Nomada banksi*, (*ruficornis* group), 212X, viewed looking down longitudinal axis of genital capsule; **Fig. 97.** Penis valves of *N. glaberrima*, (*integra* group), 195X, ventral view.

DESCRIPTIONS OF SPECIES GROUPS

The descriptions of species groups follow the general format of the preceding section. Characters printed in italics in the descriptions are those most useful for identifying the group, and can be considered as a diagnosis imbedded within the overall description. Table 3 summarizes these diagnostic characters for each group in a format intended to facilitate comparisons among groups. This table is presented in place of a dichotomous key because so many of the diagnostic features of the species groups recognized herein are male genitalic characters that are only visible upon dissection. Nevertheless, some externally visible characters are helpful in at least narrowing the range of choices in making an identification. Placing all the characters together in a table enables one to choose whichever character one prefers in starting the process of identification. However, female specimens may be impossible to decisively assign to a species group if they cannot be associated with a male.

Genus *Nomada* Scopoli

Nomada Scopoli, 1770: 44. Type species: *Apis ruficornis* Linnaeus, 1758; designated by Curtis, 1832. It is irrelevant that we do not know with certainty whether Scopoli or Curtis identified *ruficornis* correctly (International Code of Zoological Nomenclature, Article 70a). The identity of *Apis ruficornis* Linnaeus is now clear (Day, 1979). The name *Nomada* was incorrectly attributed to Fabricius (1775) by certain authors in the past.

gigas group

DESCRIPTION: (a) Labrum L/W < 1; (b) mandible simple, apex narrowly rounded; (c) first flagellomere about as long as second in male, distinctly longer than second in female; (d) preoccipital ridge angulate; (e) postocciput not distinctly recessed below level of postgenal bridge; (f) base of proboscideal fossa broadly rounded; (g) malar space closed posteriorly; (h) median portion of pronotal collar greatly narrowed, appressed against scutum; (i) lateral portion of pronotal collar rounded when viewed from front, but angulate along the crest of the curve; (j) lateral ridge of pronotum distinct, extending straight up onto neck of pronotum; (k) anterior margin of pronotum evenly rounded in profile; (l) no distinct flange on neck of pronotum; (m) metapleuron not protuberant above; (n) ridge above propodeal spiracle absent or very weak; (o) scutellum with distinct dorsal and posterior faces, bigibbous; (p) sculpturing of propodeal enclosure rugose basally (more weakly in male than in female), shagreened apically; (q) lateral margin of propodeal enclosure not delineated by a distinct ridge or carina; (r) procoxal spine absent; (s) no carina on lateral face of procoxa; (t) metasomal terga closely and distinctly punctate; (u) apical margin of metasomal terga with a very narrow impunctate area; (v,w) forewing with three submarginal cells; (x) apex of marginal cell variable, but generally narrowly rounded, in contact with costal margin of wing; (y) vestiture generally rather sparse, no unusual vestiture on propodeum. **Females**: (A) paraocular ridge present; (B) no spinose setae on outer face of hind tibia (there are prominent tubercles bearing short, apically pointed setae); (C) pseudopygidium of the typical *Nomada* form; (D) pygidial plate tapering to a narrowly rounded apex; (E) distal setae of hind tibia short, stiff, spinose, as in most other *Nomada*. **Males:** (F) anterior articulation of mandible with distinct flange; (G) scape cylindrical, about as wide as flagellum; (H) oblique frontal ridge absent; (I) protarsal brush present, setae long and prominent; (J) front femur not specially modified; (K) no flocculus or other specially modified setae at base of hind femur; (L) *subgenital brush absent (a few very tiny, inconspicuous, simple setae may be discerned near the apical margin of S6)*; (M) apical margin of S6 broadly rounded, moderately produced medially; (N) no dense subapical fringe of setae on metasomal sterna; (O) apex of pygidial plate

Table 3. Diagnostic characters for the species groups of *Nomada*. Characters shown in **underlined boldface** for a given group are those most useful for recognizing that group (although they are not necessarily unique to the group). More than one entry in a column for a given group means that the group exhibits more than one state for that character.

	EXTERNAL CHARACTERS OF MALES																
	gigas	integra	adducta	vincta	odontophora	vegana	robertsoniana	erigeronis	ruficornis	rodecki	armata	beltragei	superba	basalis	bifasciata	trispinosa	furva
ANTENNAL SCAPE																	
a) cylindrical, as wide as or wider than flagellum (Figs. 25-28)	a	a	a	a	a	a	a	a-5	a-5	a	a-5	a	a	a	a-5	a	a-5
b) subglobose, greatly enlarged (Fig. 29)			**b** 6	**b** 6													
OBLIQUE FRONTAL RIDGE																	
a) absent	a	a	a	a	a	a	a	a	a	a		a	a	a	a	a	a
b) present (Fig. 33)											**b**						
MALAR SPACE																	
a) closed posteriorly in both sexes (Fig. 34)	a	a	a	a	a	a	a	a	a	a	a	a		a	a	a	a
b) open posteriorly in male (Fig. 35) (sometimes also in female)													**b**	**b**			
BASE OF HIND FEMUR																	
a) with no unusually modified setae	a	a	a	a	a	a	a	a	a	a		a	a	a			a
b) femur with shallow ventral depression and flocculus (Fig. 66)		**b**									**b**						**b**
c) tuft of long, erect setae on trochanter, depression with recumbent setae on femur (Fig. 67)															**c**		
d) anterior and posterior margin of ventral face of femur with row of long, plumose setae (Fig. 65)																**d**	
SUBGENITAL BRUSH																	
a) absent	**a**																
b) setae very short and simple			b	b	b		b			b							
c) setae longer, suberect mesally and semi-recumbent laterally (Fig. 7b)		c							c		c	c	c	c		c	
d) median tuft absent or very short, lateral tufts conspicuous (Fig. 7g)																**d**	**d**
e) setae long, erect, often recurved apically (Figs. 7a,c,d)						**e**	**e**										
f) setae as in e), clustered either as 2 closely-packed tufts or a single dense tuft (Figs. 7e,f, 69)								**f**									
g) setae long, dense, plumose, horizontallydirected, forming apical fringe on S6 (Fig. 7h)															**g**	**g**	
SUBAPICAL SETAL FRINGE ON METASOMAL STERNA																	
a) absent; no unusually modified setae	a	a	a	a	a	a	a		a	a	a	a	a		a	a	a
b) present; setae long, erect (Fig. 7e)							**b**	**b**					**b**	**b**			
c) present; setae long, appressed (Figs. 7f, 69)							**c**										

5 -- In these groups, scape may be much wider than flagellum, completely enclosing pedicel (this is consistently so in *erigeronis* group, and is common in *ruficornis* group).

6 -- Scape subglobose in *adducta* and *brewsterae* of *adducta* group, and in all members of *vincta* group except *dreisbachorum* (males unknown for *saltillo* and *vitticollis*).

Table 3. (continued)

EXTERNAL CHARACTERS OF BOTH SEXES OR OF FEMALES ONLY

	gigas	integra	adducta	vincta	odontophora	vegana	roberjeotiana	erigeronis	ruficornis	rodecki	armata	belfragei	superba	basalis	bifasciata	trispinosa	furva
GEOGRAPHIC DISTRIBUTION																	
AF=sub-Saharan Africa; sa=South Africa;	**sa**		NA		PA		HA		HA	NA	PA		HA		PA		PA
AU=Australian; HA=Holarctic; NA=Nearctic;		PA		NA		NA	**AF**	NA	AF?			NA		PA		PA	**OR**
NT=Neotropical; OR=Oriental; PA=Palearctic						**NT**	**sa**		OR?					NA?			**AU**
ANTERIOR MARGIN OF PRONOTUM																	
a) evenly rounded in profile (Fig. 38)	a	a	a	a	a			a	a	a	a	a	a	a	a	a	a
b) distinctly angulate in profile (Fig. 36)						**b**	**b**										
SCULPTURING OF PROPODEAL TRIANGLE																	
a) very finely sculptured throughout (see descriptions and Figs. 40, 41)			a		a	a	a			a		a	a	a			
b) rugose or reticulate basally, granulose or shagreened apically (see descriptions and Fig. 42,43)	b			b			b	b	b		b		b	b	b	b	b
c) rugose or reticulate basally, polished apically (Fig. 39)		c	c-1														c-1
d) rugose throughout																	d
e) polished throughout					e-2												
PROCOXAL SPINE																	
a) absent	a	a	a	a			a		a	a	a	a	a	a	a	a	a
b) present (Figs. 44-47)				b	b	b	b	b	b								
FEMALE PARAOCULAR RIDGE																	
a) absent (Fig. 51)					**a**	**a**						**a**					
b) present (Fig. 52)	b	b	b	b			b	b	b	?	b		b	b	b	b	b
FEMALE T5																	
a) apical margin with prepygidial fimbria (Fig. 6)	a	a	a	a		a	a-3	a	a-3	?	a	a	a	a	a	a	a
b) pair of cuticular denticles in place of prepygidial fimbria					**b**												
FEMALE PYGIDIAL PLATE																	
a) narrowly rounded apically (Fig. 59)	a	a	a	a	a	a	a	a	a	?	a	a			a		a
b) broadly rounded apically (Fig. 60)						**b**							**b**	**b**		**b**	
APICAL SETAE ON FEMALE HIND TIBIA																	
a) stout, spinose, cylindrical or flattened (Fig. 53)	a	a	a	a	a	a	a	a	a	?	a-4	a					a
b) short, stout, peglike, heavily melanized (Fig. 55)																**b**	
c) dense cluster of stout, straight, flattened setae arising from flattened area (Fig. 54)											**c**-4						
d) long, narrow, in dense cluster of ca. 10-25 setae (Figs., 56,57)													**d**	**d**			
e) broad, flate, bladelike, apically curved, imbricate (Fig. 58)															**e**		

1 -- Only one species in *adducta* group, viz.*brewsterae*, has " type c" sculpturing. Many species in *furva* group have sculpturing that is "type c" or intermediate between "type b" and "type c".

2 -- Male of *argentea* has this type of sculpturing.

3 -- North American species *depressa* (=*depressicauda*), *velutina*, and *angulata* , all in *ruficornis* group, have prepygidial fimbria much broader than in other *Nomada*, with a velvety appearance. South African species *N. whiteheadi*, in *roberjeotiana* group, has no distinct fimbria, only a sparse row of thick black setae.

4 -- *armata* group species with "type c" setae are *fuscicornis*, *linsenmaieri*, *merceti*, *nitida*, *panurgina*, *panurginoides* (weak) *polyacantha*, *rubricoxa*, *rufoabdominalis*, *sicula*, *similis*.

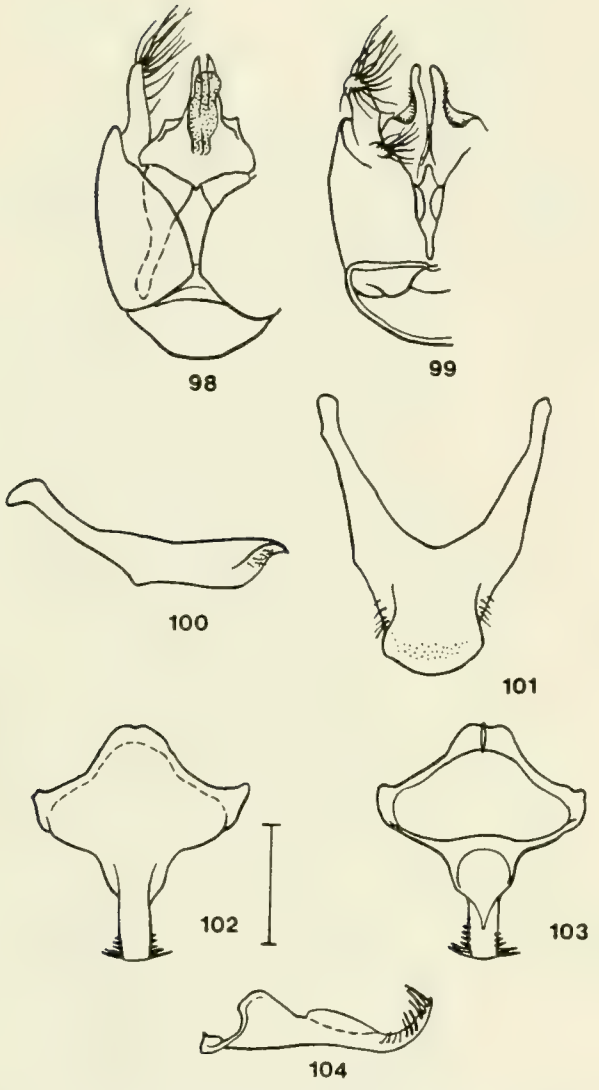
Table 3. (continued)

	gigas	integra	adducta	vincta	odontophora	vegana	roberjeotiana	erigeronis	ruficornis	rodecki	armata	balfragei	superba	basalis	bifasciata	trispinosa	furva
INTERNAL CHARACTERS OF MALES (S7, S8, GENITAL CAPSULE)																	
SHAPE OF S7																	
a) apodemes moderately long, disc of sternum subtriangular, apical margin rounded or subtruncate (Figs. 73-75)			a	a	a	a	a	a	a	?	a	a	a	a	a	a	a
b) apodemes as in a), but apex a broad, spatulate structure (Figs. 100, 101)	b																
c) apodemes as in a), but apical margins laterally compressed, may also be recurved or with ventromedian keel											c						
d) apodemes long and narrow, disc of sternum narrowed to process that is rectangular or has concave sides		d															
MEDIAN PROCESS OF S8																	
a) dorsoventrally compressed, short and broad, apex broadly rounded (Fig. 76)							a	a									
b) dorsoventrally compressed, but long and narrow, apex narrowly rounded (Figs. 77, 78)			b	b		b											
c) laterally compressed, long, narrow, parallel-sided, often expanded apically (Figs. 80-83)	c	c			c				c		c	c	c	c	c	c	
d) as in c), but process very short, distinctly expanded apically (Fig. 79)																	d
e) laterally compressed, tapering from base to truncate, recurved apex										e							
VENTRAL HOOK ON PENIS VALVE																	
a) absent	a	a	a			a	a	a	a	a	a	a	a	a	a	a	a
b) present (Figs. 93, 122-123,127)				b	b												
INNER RIDGE ON PENIS VALVE																	
a) absent (Figs. 88, 96)	a	a	a			a	a	a	a	a	a	a	a	a	a	a	a
b) present (Figs. 93, 124-126,129)				b	b												
OUTER RIDGE ON PENIS VALVE																	
a) absent (Figs. 96, 97)		a	a						a	a	a	a	a	a	a	a	a
b) present, broadly rounded, welt-like (Fig. 93)				b	b												
c) present, angulate or carinate (Figs. 94, 95)						c	c	c									
d) present, a carinate sinuous ridge (Figs. 98, 99)	d																
APEX OF PENIS VALVE																	
a) acute (Figs. 94, 96)	a		a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
b) rounded, or modified into a pincerlike structure (Figs. 97, 114)		b															
PENIS VALVE LATERAL PROFILE																	
a) distad of basal apodeme (to right of apodeme on Fig. 85): subtriangular, strongly tapering to narrow apex	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a		a
b) distad of basal apodeme: long, narrow, very gradually tapering to apex (Fig. 84)																b	
INVAGINATION OF DORSAL GONOCOXITE																	
a) absent (Fig. 130)								a									
b) present (Fig. 88)		b	b	b	b	b	b		b	b	b	b	b	b	b	b	b
c) median sinus broadly V-shaped, invagination very shallow or absent (Fig. 98)	c																

Table 3. (continued)

	gigas	integra	adducta	vincta	odontophora	vegana	roberjeotiana	erigeronis	ruficornis	rodecki	armata	belfragei	superba	basalis	bifasciata	trispinosa	furva
INTERNAL CHARACTERS OF MALES (S7, S8, GENITAL CAPSULE)																	
INNER DORSAL LOBE OF GONOCOXITE																	
a) absent or very weak (Figs. 130, 131)	a							a									
b) present, about as long as broad (Figs. 88, 90)		b	b		b	b-7	b		b	b	b	b	b	b	b	b	b
c) present, much longer than broad (Fig. 133)		c				c											
d) present, much broader than long and median sinus very narrow (Fig. 121)				d													
SHAPE OF GONOSTYLUS																	
a) cylindrical, long, narrow, apex rounded but not expanded (Fig. 87, 98, 117)	a		a	a	a	a	a	a									
b) cylindrical, short, broad, apex blunt and rounded (Flgs. 86, 88-91, 133-135)						b			b	b	b	b	b				
c) as in a), but curved strongly mesad (Figs. 172,173)																c	c
d) flattened or triangular in cross section, apical portion often curved mesad (Figs. 110-116)		d															
e) apical half flattened and curved strongly mesad, apex often obliquely truncate (Figs. 166-168)															e		
f) shape irregular, usually with apical portion much narrower than base and curved mesad (Figs. 149-152, 154)														f			
VESTITURE OF GONOSTYLUS																	
a) sparse, simple, some setae more than half as long as gonostylus, uniformly distributed around gonostylus (Figs. 133-135)	a	a				a	a										
b) as in a), but setae arising only from apex and ventral face of gonostylus (Figs. 130-132)								b			b						
c) sparse, simple, setae short, less than half as long as gonostylus (Figs. 87, 121-123, 127,128)			c	c	c												
d) very long, dense, apically plumose or sinuate, not divided into separate tufts (Figs. 86, 88-91)									d	d	d	d	d				
e) as in d), but divided into distinct basal and apical tufts (Figs. 172-174)														e		e	e
f) as in e), but apical tuft subdivided (Figs. 166-168)															f		
BASOVENTRAL LOBE ON GONOSTYLUS																	
a) absent (Figs. 131,132,134,135)		a	a		a	a	a	a			a						
b) present, hemispherical (Figs. 99, 122, 123)	b			b								b					
c) present, cylindrical (Figs. 90, 91)									c	c	c		c	c	c		
d) present, transverse ridge (Fig. 173)														d		d	d
SCLEROTIZED PATCH ON MESAL FACE OF GONOSTYLUS																	
a) absent (Flgs. 143,145)	a	a	a	a	a	a	a	a	a	a		a	a	a	a	a	a
b) present (Fig. 148)											b						

7 --Even when inner lobe is short, gonocoxite laterad of invagination is long and narrow (Fig. 133, see text for details).



Figs. 98-104: Male genitalia and associated sterna of *Nomada gigas*. **Fig. 98**. Genital capsule, dorsal view; **Fig. 99.** Same, ventral view; **Fig. 100.** S7, lateral view; **Fig. 101.** S7, ventral view; **Fig. 102.** S8, ventral view; **Fig. 103**. S8, dorsal view; **Fig. 104**. S8, lateral view. Scale bar = 0.5 mm.

subtruncate; (P) *metasomal sternum 7 unique and distinctive, with a broad, spatulate median process* (Figures 100, 101); (Q) median process of S8 parallel-sided, fairly broad, recurved but not widened apically, more or less laterally compressed basally, but dorsoventrally compressed apically (Figures 102-104); (R) median process of S8 in same plane as base of S8; (S) stout, spinose setae present on median process of S8; (T) gonostylus cylindrical in cross section, long, narrow, and straight (Figure 98); (U) no inner basal shelf on gonostylus; (V) vestiture of gonostylus sparse, setae simple, about as long as gonostylus, (W,X) ventral base of gonostylus with a weak lobe bearing a distinct tuft of long, simple setae (Figure 99); (Y) gonobase not reduced in size; (Z) no ventral hook on penis valves; (AA) no inner ridge on penis valves; (BB) *outer ridge on penis valve distinct and unique, comprising a carinate sinuous ridge as shown in Figures 98 and 99*; (CC) penis valves not dorsally flattened; (DD) no basoventral swelling on penis valves; (EE) apex of penis valves greatly narrowed, subacute; (FF,GG) *invagination of dorsal gonocoxite extremely shallow* (as in Figure 6 of Eardley and Schwarz, 1991) *or absent* (as in Figure 98); *median sinus broadly V-shaped, so that there is no distinct inner, basal lobe of the gonocoxite.*

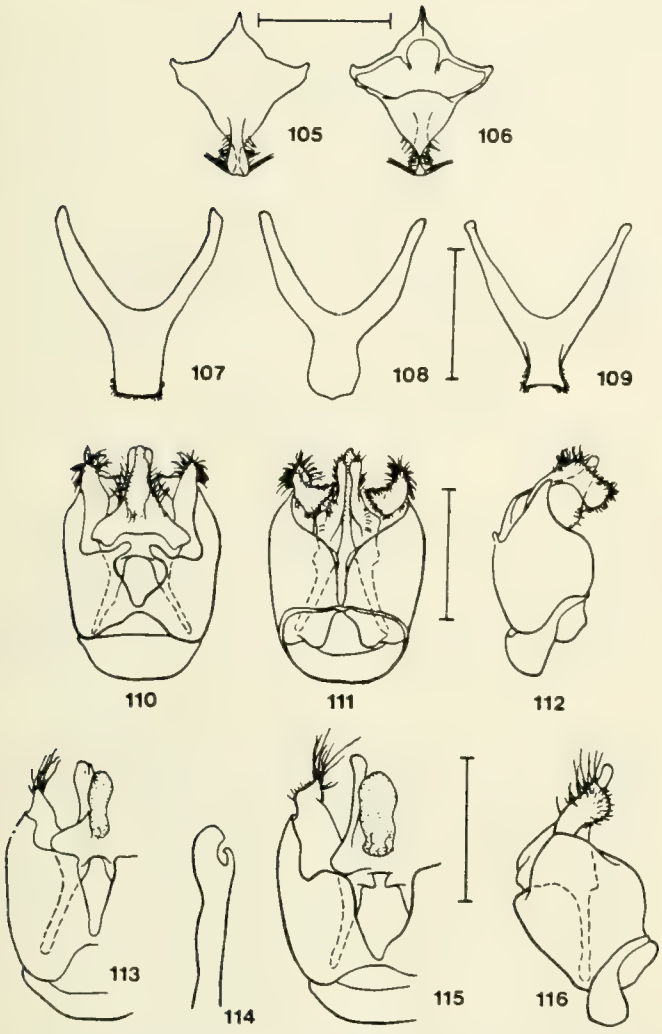
COMMENTS: The cladistic analyses indicate that this species is the basal lineage in the genus *Nomada*. This conclusion should be viewed with considerable skepticism, however. My coding of the dorsal invagination of the male gonocoxite is based upon an examination of only seven specimens, and the distinctness of the invagination varies considerably even in this small sample. If the invagination were to be coded not as an autapomorphy of *N. gigas* (as it was in the cladistic analyses), but as falling within the range of variation of those taxa in which the invagination is simply coded as present, the only remaining argument for the basal placement of *gigas* would be the absence of the subgenital brush and the inner dorsal lobe of the gonocoxite. The question of independence of the latter character from the dorsal invagination of the gonocoxite is discussed in the Cladistic Analysis section. My phylogenetic interpretation of the median process of S8 could also be challenged, since this structure (Figures 102-104) exhibits aspects of two common states, coded as 2 and 3 in the cladistic analyses. It was coded as state 3 for the cladistic analyses (an interpretation that would argue *against* a basal placement for *gigas*).

BIOLOGY: Brauns (1930) reported *Melitta capensis* (Family Melittidae) as a probable host of *Nomada gigas* (erroneously referred to at one point in Brauns' paper as *N. gigantea*). The only evidence for the association is that Brauns frequently found the two species occurring together in the winter of 1917. If this record is correct, it is an unusual host association for a species of *Nomada*. To my knowledge, the only other *Nomada* species suggested to be a parasite of *Melitta* is the European species *N. flavopicta*, in the *ruficornis* group, and this association is also based on indirect evidence (Stoeckhert, 1932).

integra group

cinctiventris group, Schwarz, 1967: 263. (*integra* Brullé is a senior synonym of *cinctiventris* Friese; synonymy in Schwarz, 1986, Entomofauna 7: 461-462).

DESCRIPTION: (a) Labrum L/W < 1; (b) mandible simple, apex acutely rounded or subacute; (c) relative length of first vs. second flagellomere variable: usually first shorter than second, especially in males, but segments roughly equal in females of several species, and first segment longer than second in *glaberrima* and some females of *nigra*; (d) preoccipital ridge variable: rounded, angulate, or carinate; (e) postocciput not sharply recessed below level of postgenal bridge; (f) base of proboscideal fossa broadly rounded (except in *glaberrima*); (g) malar space closed posteriorly; (h) median portion of pronotal collar angulate (except in *glaberrima*, which possesses a unique state); (i) lateral angle of pronotal collar with an angulate crest (rounded in *glaberrima*); (j) lateral ridge of pronotum weak or absent (except in *glaberrima*, which resembles Neotropical species of the *vegana* group); (k) anterior margin of pronotum either rounded or angulate (may vary even within species); (l) no recurved flange on neck of pronotum; (m) upper region of metapleuron usually not protuberant (occasionally protuberant in *argentata* and *tridentirostris*); (n) no ridge above propodeal spiracle; (o) scutellum usually with distinct dorsal and posterior faces, occasionally evenly rounded; (p) *sculpturing of propodeal enclosure shining, smooth or weakly shagreened, with distinct, fine wrinkles basally (i.e. adjacent to metanotum) in parallel, reticulate, or radial patterns* (Figure 39, also Figures 7, 99, 135 in Schwarz, 1967); (q) no carina marking lateral margins of propodeal enclosure (a very weak, incomplete margin is sometimes present in *argentata*, *beaumonti*, and *carthaginensis*); (r) no spine on procoxa; (s) procoxa without carinae on outer surface (except *glaberrima*, which has a complete lateral carina); (t) sculpturing of metasomal terga



Figs. 105-116: Male genitalia and associated sterna for *integra* group. **Fig. 105.** S8, ventral view, *Nomada tridentirostris*; **Fig. 106.** Same, dorsal view; **Fig. 107**. S7, ventral view, *N. stigma*; **Fig. 108**. Same, *N. facilis*; **Fig. 109.** Same, *N. tridentirostris*; **Fig. 110.** Genital capsule, dorsal view, *N. tridentirostris;* **Fig. 111**. Same, ventral view; **Fig. 112.** Same, lateral view; **Fig. 113**. Genital capsule, dorsal view, *N. beaumonti;* **Fig. 114.** Apex of penis valve, *N. beaumonti.*; **Fig. 115.** Genital capsule, dorsal view, *N. argentata;* **Fig. 116**. Same, lateral view. Scale bar represents 0.5 mm for all figures except 114, for which it represents 0.25 mm.

variable: punctures usually weak and sparse, but denser and closer in *pleurosticta, rubricollis*, and *stigma*; (u) apical margin of metasomal terga with a broad impunctate or sparsely punctate area; (v,w) three submarginal cells present (vein 1st r-m occasionally missing, resulting in two submarginal cells, in *pleurosticta*); (x) apex of marginal cell pointed, ending on costal margin of forewing. **Females**: (A) paraocular ridge present (except in *glaberrima*); (B) without spinose setae on outer face of hind tibia; (C) pseudopygidium of typical *Nomada* form; (D) pygidial plate tapering to a narrowly rounded apex; (E) distal setae of hind tibia spinose, subtly varying among species, but not exhibiting a group-level apomorphic state. **Males**: (F) anterior articulation of mandible with a distinct, recurved flange (sometimes almost disclike in *argentata*); (G) scape never conspicuously enlarged, but usually slightly wider than flagellum; (H) no oblique frontal ridge; (I) protarsal brush present (weak in *argentata* and usually in *thersites*); (J) front femur not conspicuously enlarged or flattened; (K) base of hind femur variable, often concave ventrally, and bearing a dense flocculus in *integra, facilis, imperfecta, nigra, pallispinosa, pleurosticta*, and (weakly) in *rubiginosa*; flocculus absent in *amathusica, argentata, beaumonti, carthaginensis, caspia, glaberrima, rubricosa, stigma*, and *tridentirostris*; (L) subgenital brush with setae moderately long, suberect mesally and more nearly recumbent laterally; (M) apex of S6 produced, broadly rounded medially; (N) no apical fringe of setae on sterna; (O) apex of pygidial plate variable, even within species (only *glaberrima* consistently has a distinct notch); (P) *S7 with relatively long, narrow apodemes and with parallel-sided, subtruncate median apical process* (Figures 107-109, also illustrated in Schwarz, 1967). Sometimes the median process is weakly concave (Figure 109) or convex (Figure 108) apically; (Q,R,S) median process of S8 laterally compressed, parallel-sided basally, but relatively broad and apically expanded (Figures 105, 106, also illustrated in Schwarz, 1967), median process bearing spinose setae and lying in same plane as disc of sternum; (T) *shape of gonostylus variable, but consistently flattened rather than cylindrical, not like the gonostyli of any other* Nomada *(Figures 111, 112, 116);* (U) no inner basal shelf on gonostylus; (V) vestiture of gonostylus always sparse, usually short (e.g. *tridentirostris*, Figures 110-112), but occasionally long and weakly sinuous apically (e.g. *argentata*, Figures 115, 116); (W) no basoventral lobe on gonostylus; (X) no basoventral setal tuft on gonostylus; (Y) basal ring of genital capsule not conspicuously reduced; (Z) no ventral hook on penis valves; (AA) no inner ridge on penis valves; (BB) no outer lateral ridge on penis valves; (CC) penis valves not dorsally flattened; (DD) no basoventral swelling on penis valves; (EE) *apex of penis valves bluntly rounded, or further modified into pincerlike structures as in* beaumonti, carthaginensis, *or* caspia *(Figures 97, 112, 114, 116, also Figures 35, 42, 131 in Schwarz, 1967)*; (FF,GG) invagination of dorsal gonocoxite present (except in *stigma*), *inner dorsal lobe of gonocoxite often bearing a very thin, nipplelike process* (when this process is absent there is often a sharp angle in the position where the process would be, see Figures 110, 113, 115, and illustrations in Schwarz, 1967).

COMMENTS: The sculpturing of the propodeal enclosure is externally visible and present in both sexes, but difficult to distinguish from similar states in other groups. Many species in the *furva* group have the apical portion of the propodeal enclosure polished, but the basal portion tends to be more coarsely sculptured, and the rugae are often reticulate rather than parallel. The basal rugae are of the latter form in many species of the *ruficornis* group, but the apical portion tends to be dull rather than shiny, and is usually more heavily sculptured (cf. Figures 39, 43). The one known specimen of *Nomada brewsterae* (in the *adducta* group) has sculpturing of the propodeal enclosure similar to that of the *integra* group. If the propodeal sculpturing were the only putative autapomorphy for the *integra* group, I would consider its monophyly doubtful. However, the autapomorphies of the male genitalia that are diagnostic for this group are quite striking and provide strong evidence that it is monophyletic. Unlike most other *Nomada*, male genitalia in this group vary enough among species to have been used extensively in species-level taxonomy (Schwarz, 1967). Frequently, the male antennae also bear unusual species-specific modifications (see figures in Schwarz, 1967), but similar variability in male antennae also occurs in the *erigeronis* and *ruficornis* groups.

Species of the *integra* group are restricted to the Palearctic region, with the highest diversity in the Mediterranean region. The species *glaberrima* is placed in this group because it has all the hypothesized autapomorphies, although in overall appearance it is quite aberrant and shows a few intriguing similarities to South American species of the *vegana* group. These similarities are interpreted as cases of homoplasy, since they involve character states (such as

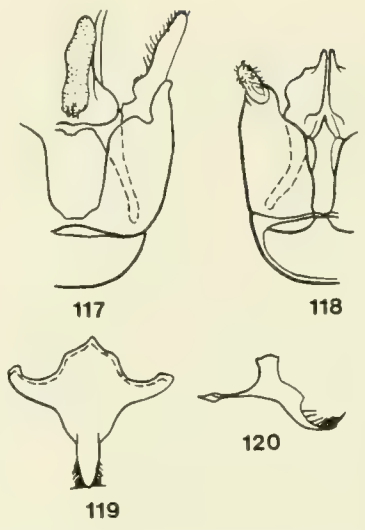
the loss of the paraocular ridge in females, a constriction at the base of the proboscideal fossa, and a complete ridge on the outer face of the procoxa) that are also found sporadically in other species in other groups.

BIOLOGY: In his revision of this group, Schwarz (1967) provided host records for five species. Westrich (1989) noted a few additional records not reported by Schwarz. As with most records from the European literature, these associations are apparently based on indirect evidence such as repeated observations of the parasites on flowers also frequented by the suspected hosts, or in the nest areas of their putative hosts, rather than on the direct evidence of rearing parasites from nests of their hosts. All the reported hosts are species of *Andrena*, summarized as follows: *Andrena humilis* for *Nomada integra*; *A. polita* for *N. pleurosticta*; *A. marginata* for *N. argentata*; *A. labialis*, *A. schencki*, and *A. decipiens* for *N. stigma*; *A.* sp. aff. *variabilis* for *N. stigma cypricola*; and perhaps *A. humilis* and *A. labialis* for *N. facilis*.

adducta group

Nomada subgenus *Asteronomada* Broemeling, 1988. Pan-Pac. Entomol. 64: 336-338. Type species: *Nomada adducta* Cresson, 1878; original designation.

DESCRIPTION: (a) L/W labrum < 1; (b) apex of mandible simple, narrowly rounded; (c) first flagellomere distinctly longer than second; (d) preoccipital ridge rounded or weakly angulate; (e) postocciput not distinctly recessed below level of postgenal bridge between posterior tentorial pits (somewhat recessed in *adducta*, but not as distinctly as in *vegana* group); (f) base of proboscideal fossa broadly rounded; (g) malar space closed posteriorly; (h) median portion of pronotal collar sharply angulate; (i) lateral portion of pronotal collar rounded when viewed from in front, angulate along crest of curve; (j) lateral ridge of pronotum weak, extending straight up towards neck of pronotum; (k) anterior margin of pronotum evenly rounded in profile; (l) no distinct flange on neck of pronotum; (m) metapleuron not protuberant above; (n) no ridge above propodeal spiracle; (o) scutellum with distinct dorsal and posterior faces; (p) sculpturing of propodeal enclosure variable (not recorded for *portalensis*): rugose basally, shagreened apically in *adducta* and *brewsterae*, with rugae in a whorled, "fingerprint" pattern (especially striking in *brewsterae*); sculpturing much finer in *durangoae*, but the very fine rugulae are arranged in a similar pattern; (q) no distinct ridge or carina marking lateral margin of propodeal enclosure; (r) procoxal spine absent; (s) no lateral carina on procoxa; (t) sculpturing of metasomal terga consisting of dense, close punctures; (u) apical margins of metasomal terga variable, but usually with a distinct impunctate region (widest in *portalensis*); (v,w) forewing with three submarginal cells; (x) apex of marginal cell narrowly rounded, contacting costal margin of forewing; (y) *sides and posterior face of propodeum except for propodeal enclosure with a dense vestiture of appressed, plumose, white setae that obscure the underlying integument.* **Females**: (A) paraocular ridge present; (B) no spinose setae on outer face of hind tibia; (C) pseudopygidium of typical *Nomada* form; (D) pygidial plate tapering to a narrowly rounded apex; (E) distal setae of hind tibia of typical spinose *Nomada* form, not further modified. **Males**: (F) anterior articulation of mandible with a distinct recurved flange; (G) scape variable: cylindrical, not much wider than flagellum in *durangoae* and *portalensis*, distinctly swollen and subglobose in *adducta* and *brewsterae*; (H) no oblique frontal ridge; (I) protarsal brush present, well developed; (J) front femur not unusually enlarged or modified; (K) base of hind femur not specially modified, without flocculus; (L) *subgenital brush inconspicuous, composed of dense but very short, simple or weakly plumose setae* (this state also occurs in the *vincta* and *odontophora* groups, in *Nomada rodecki*, and in many species of the *roberjeotiana* group); (M) apex of S6 moderately produced and broadly rounded mesally; (N) no dense apical fringe of setae on sterna; (O) pygidial plate subtruncate apically; (P) S7 not specially modified, broadly rounded apically; (Q,R,S) median process of S8 dorsoventrally compressed, long and narrow, tapering from base to a narrowly rounded apex, process in profile curving apically, not lying in same plane as disc of sternum, spinose setae rather dense and thin, except for one or two pair of more robust setae apically (Figures 119, 120); (T) gonostylus cylindrical in cross section, relatively long and narrow, not strongly curved toward midline of genital capsule; (U) no inner basal shelf on gonostylus; (V) *vestiture of gonostylus short (no longer than half the length of the gonostylus), sparse, and simple* (Figures 117, 118; this state also occurs in the *vincta* and *odontophora* groups); (W,X) no basoventral lobe or setal tuft on gonostylus; (Y) gonobase not greatly reduced; (Z) no ventral hook on penis valves; (AA) no inner ridge on penis valve; (BB) outer face of penis valve with only a short, incomplete trace of a lateral ridge; (CC) penis valve not dorsally flattened; (DD) no basoventral swelling on penis valve; (EE) apex of penis valve acute or narrowly rounded; (FF,GG) dorsal gonocoxite with shallow invagination and short, broad inner lobe (Figure 117).



Figs. 117-120: Male genitalia and associated sterna for *adducta* group. Freehand drawings of holotype of *Nomada brewsterae*, University of Colorado Museum. **Fig. 117.** Genital capsule, dorsal view; **Fig. 118.** Same, ventral view; **Fig. 119.** S8, ventral view; **Fig. 120.** S8, lateral view.

COMMENTS: Broemeling (1988, p. 388) considers this group to occupy a position "intermediate between *Pachynomada* [= *vincta* group] and *Nomadita* [= *roberjeotiana* group]". He distinguishes it from these two groups primarily by the *absence* of characters diagnostic for those groups, and he does not present any character analysis to support his inference that *Asteronomada*, *Pachynomada*, and *Nomadita* are closely related. However, one of the characters that he lists as diagnostic for *Asteronomada* may be an autapomorphy for the group. This is the vestiture of dense, appressed, plumose setae that obscure the underlying integument on the propodeum. The vestiture is much shorter in *adducta* than the other three species in Broemeling's subgenus *Asteronomada*. If this type of vestiture is not homologous for the species assigned to the *adducta* group, there is no other evidence for its monophyly. Furthermore, the species of the Old World *odontophora* group have a propodeal vestiture indistinguishable (under a stereomicroscope) from that of *adducta*. The subgenital brush of very short, simple setae is a useful diagnostic trait for this group, but this state also occurs in many species of the *roberjeotiana* group, including all of

the North American species. The swollen antennal scape of males is another clearly apomorphic trait, but it is not present in all males of the *adducta* group (or of the *vincta* group, the only other group in which this type of antennal scape occurs).

The phylogenetic placement of *adducta* has long bewildered North American students of *Nomada*, and it continues to do so. In my cladistic analyses, the *adducta* group was not consistently placed as the sister group of any other one taxon.

BIOLOGY: Species of the *adducta* group are restricted to western and central North America, and are active in late summer and early autumn. All four species are rarely collected, and two (*brewsterae* and *durangoae*) are known only from the holotypes. There are no host records for any species in this group.

vincta group

Nomada subgenus *Pachynomada* Rodeck, 1945, Entomol. News 56: 180. Type species: *Nomada vincta* Say, 1837; original designation.

DESCRIPTION: (a) L/W labrum < 1; (b) apex of mandible simple, narrowly to broadly rounded; (c) second flagellomere usually longer than first (segments equal in *asteris* and *viticollis*); (d) preoccipital ridge rounded or angulate; (e) postocciput not distinctly recessed below level of postgenal bridge; (f) base of proboscideal fossa broadly rounded; (g) malar space closed posteriorly; (h) median portion of pronotal collar usually angulate (sharply carinate in *victrix*); (i) lateral portion of pronotal collar rounded when viewed from the front, angulate or rounded along the crest of the curve (very sharply angulate in *dreisbachorum*); (j) lateral ridge of pronotum broadly rounded or absent; (k) anterior margin of pronotum evenly rounded in profile; (l) no recurved flange on neck of pronotum; (m) metapleuron not protuberant above; (n) no ridge above propodeal spiracle; (o) scutellum usually with distinct dorsal and posterior faces, but flattened, with posterior face greatly reduced, in *asteris*; (p) sculpturing of propodeal enclosure with distinct, but sometimes rather fine, rugae basally, shagreened or finely granulose apically; (q) no distinct ridge marking lateral margin of propodeal enclosure; (r) procoxal spine usually absent, but short spine present in *vincta* and *utahensis*, distinct triangular process present in *dreisbachorum*; (s) no carina consistently present on lateral face of procoxa (trace present in some specimens); (t) metasomal terga evenly and closely punctate, punctures fine and shallow (rather sparse in *besseyi*, *victrix*, and *vitticollis*), punctation partially obscured by a dense coat of very short, very fine, recumbent setae; (u) impunctate apical margin of terga very narrow (except in *victrix* and *vitticollis*, where it is somewhat wider); (v) 1st r-m of forewing usually present, but absent (resulting in two submarginal cells of roughly equal length) in *vitticollis* and *dreisbachorum*; (w) vein Rs of forewing complete; (x) apex of marginal cell narrowly rounded, ending on costal margin of forewing; (y) vestiture of propodeum variable, virtually absent to rather sparse, erect, and weakly plumose; no group-level apomorphic state. **Females**: (A) paraocular ridge usually present (absent in *asteris*); (B) no spinose setae on outer face of hind tibia; (C) pseudopygidium of typical *Nomada* form; (D) *pygidial plate parallel-sided basally, broadly U-shaped apically* (this state also occurs in the *trispinosa*, *superba* and *basalis* groups); (E) distal setae of hind tibiae short, straight, spinose, not unusually modified. **Males**: (F) anterior articulation of mandible with weak recurved flange; (G) *scape usually greatly swollen and subglobose, partially enclosing pedicel* (cylindrical, not swollen in *dreisbachorum*); (H) no oblique frontal ridge; (I) protarsal brush well developed; (J) front femur not specially modified; (K) base of hind femur unmodified, with no flocculus; (L) *subgenital brush inconspicuous, setae very short and simple, recumbent* (this state also occurs in the *adducta* and *odontophora* groups, in *Nomada rodecki*, and in many species of the *roberjeotiana* group); (M) apex of S6 moderately produced, broadly rounded mesally; (N) no dense subapical setal fringe on metasomal sterna; (O) pygidial plate usually entire (shallowly emarginate in *dreisbachorum*); (P) S7 not specially modified, apical margin broadly rounded or subtruncate; (Q,R,S) median process of S8 *dorsoventrally compressed, very long and narrow, tapering from base to a narrowly rounded apex*, with rather slender spinose setae (Figure 77); S8 not angulate in lateral profile; (T) gonostylus long, narrow, cylindrical; (U) no inner basal shelf on gonostylus; (V) *vestiture of gonostylus very short (setae less than half as long as gonostylus), sparse, simple* (Figures 87, 121-123; this state also occurs in the *adducta* and *odontophora* groups); (W) *basoventral lobe of gonostylus very short, hemispherical* (Figures 87, 122); (X) *setal tuft at ventral base of gonostylus comprised of short, simple setae* (Figures 87, 122); (Y) gonobase not distinctly reduced; (Z) *ventral hook present on penis valve, not directed mesally, distinctly visible in lateral view* (Figures 122, 123, arrow, 93, **vh**); (AA) *distinct ridge present on inner face of penis valve, sometimes slightly produced basally* (Figures 124-126, arrow); (BB) *outer lateral ridge present on penis valve, generally rounded or angulate, not distinctly carinate* (Figures 93 **or**, 124-126); (CC) penis valve not dorsally flattened; (DD) no basoventral swelling on penis valve; (EE) apex of penis valves acute; (FF,GG) invagination on dorsal gonocoxite shallow or almost absent, *inner lobe very short and broad, so that median sinus is very narrow and slitlike* (Figure 121).

COMMENTS: Males of most species in this group are readily recognizable by their distinctly swollen, subglobose antennal scape, which Rodeck (1945) regarded as a diagnostic trait for his subgenus *Pachynomada*. However, this character also occurs in some species of the *adducta* group. Furthermore, in *dreisbachorum*, a species unknown to Rodeck, the scape is cylindrical and not much wider than the flagellum. Nevertheless, *dreisbachorum* has the ventral hook on the penis valve, a character which reliably separates species of the *vincta* group from those of the *adducta* group. The broad inner dorsal lobe of the gonocoxite and narrow, parallel-sided median sinus are also diagnostic, and apparently apomorphic, for the *vincta* group.

My cladistic analyses suggest a sister-group relationship between the *vincta* and *odontophora* groups, which is supported by similarities in certain features of the penis valves that are found only in these groups. (The *odontophora* group also has many striking autapomorphies.) Because the current geographic distributions of these two groups represent an unusual disjunction (North America and Asia Minor), and because the two groups show no special similarities in features other than those of the male genitalia, there is good reason to question whether the similarities in the penis valve characters are homologous. However, discernible differences in the structures in the two groups are subtle. In the *vincta* group, the hooklike process on the penis valve lies in roughly the same plane as the valve (Figures 93, 122), whereas in the *odontophora* group the hook is directed mesad. The difference is most apparent when the valves are viewed from the side, since the hook is clearly visible in the *vincta* group (Figure 123), but barely discernible in the *odontophora* group. The ridge on the inner face of the penis valve, near the articulation of the aedeagus with the valves, has a very narrow, toothlike process basally in the *odontophora* group (Figure 129, arrow). The ridge is variable in the *vincta* group, occasionally possessing a weak process basally (Figures 93, 124, 126). The ridge on the outer face of the penis valve is more difficult to describe, so the differences are not easily characterized; but the ridge seems more sharply angulate or subcarinate in the *odontophora* group (compare Figures 127, 124-126, 93). Because these differences are so subtle, I did not recode them as separate states in the two groups; but I would call attention to the possibility that they are not homologous, and thus that the *vincta* and *odontophora* groups are not sister taxa.

Females of the *vincta* group are not easy to distinguish from some in the *ruficornis* group. Several species were formerly placed in the *superba* group (= subgenus *Holonomada*), primarily on the basis of

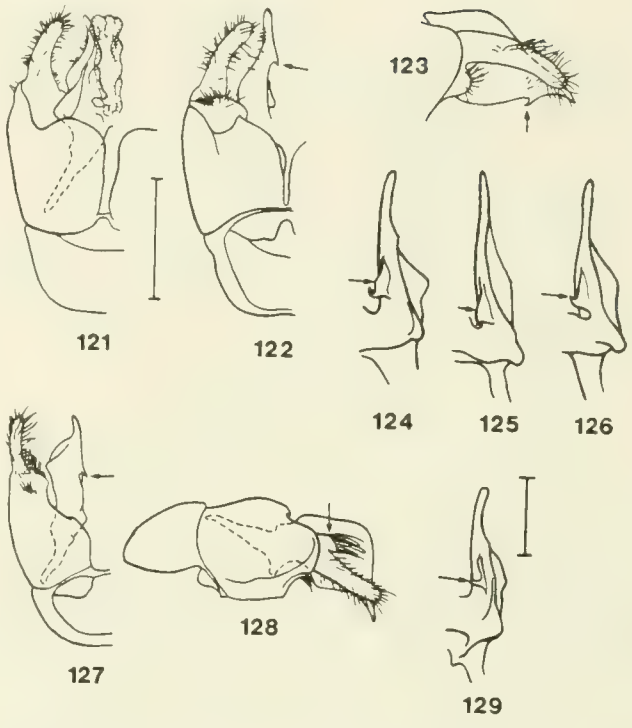
their broadly rounded pygidial plate. However, females in the *superba* group have apomorphic traits, such as the distal setae of the hind tibia, that are not present in the *vincta* group. The hind basitarsus in the *vincta* group is somewhat swollen in appearance, being widest near the middle rather than at the base, but this is a very subtle character. The *vincta* group is restricted to North America, extending as far south as central Mexico. The greatest species diversity is in Mexico, with only *vincta* occurring east of the Mississippi River in the U.S. This group was recently revised by Broemeling and Moalif (1988), who recognized fourteen species and subspecies. It is likely that a more detailed survey of Mexico's bee fauna would uncover more species, since I have seen two Mexican specimens that do not seem to correspond to any of the species described by Broemeling and Moalif.

BIOLOGY: The species of the *vincta* group are rare, and very little is known about their biology, apart from the observation that they have been collected in mid- to late summer. Parker and Bohart (1982) reported *Nomada utahensis* as a parasite of *Andrena helianthi*, and it may also parasitize *Andrena haynesi* in Utah (Parker and Griswold, 1982).

odontophora group

Acanthonomada Schwarz, 1966. Polskie Pismo Entomol. 36: 383. Type species: *Nomada odontophora* Kohl, 1905; original designation.
Nomada subgenus *Acanthonomada* Warncke, 1982. Entomofauna 3: 103.

DESCRIPTION: (a) *L/W labrum > 1* (also occurs in some species of the *vegana, furva,* and *armata* groups); (b) apex of mandible simple, narrowly rounded; (c) first flagellomere longer than second; (d) preoccipital ridge distinctly carinate; (e) postocciput not distinctly recessed below level of postgenal bridge; (f) base of proboscideal fossa distinctly narrowed, slitlike; (g) malar space closed posteriorly; (h) median portion of pronotal collar carinate; (i) lateral portion of protontal collar rounded when viewed from in front, but angulate along the crest of the curve; (j) lateral ridge of pronotum absent or very weak; (k) anterior margin of pronotum weakly angulate in profile; (l) no distinct flange on neck of pronotum; (m) metapleuron not protuberant above; (n) no ridge above propodeal spiracle; (o) scutellum greatly flattened, lacking a distinct posterior face; (p) *integument of propodeal enclosure shining, with an extremely faint shagreened texture, no basal rugae;* (q) no ridge marking lateral margins of propodeal enclosure; (r) procoxal spine inconspicuous, a short, triangular, apically acute process; (s) complete, distinct carina present on outer face of procoxa; (t,u) metasomal terga with distinct, fine punctures that are very densely spaced basally, becoming progressively sparser apically, with recessed apical margin of terga impunctate and polished; (v,w) forewing with three submarginal cells; (x) apex of marginal cell broadly rounded, slightly removed from costal margin of forewing; (y) *vestiture, especially on propodeum and mesepisternum, of very short, appressed, densely plumose, white setae that obscure the underlying integument and give an overall silvery appearance to the sides of the mesosoma; vestiture denser in male than in female* (this same vestiture also occurs in the *adducta* group). **Females**: (A) paraocular ridge absent; (B) *outer surface of hind (and middle) tibiae bearing short, stout, apically pointed spinose setae* (see Figures 20 and 21 in Schwarz, 1966; similar setae occur in some neotropical species of the *vegana* group); (C) *apex of T5 without a prepygidial fimbria of modified setae, but with a pair of minute cuticular denticles mesally near the apical margin;* (D) pygidial plate tapering to a narrowly rounded apex; (E) distal setae of hind tibia short, stout, straight, pointed at apex. **Males**: (F) very weak flange at anterior articulation of mandible; (G) scape subcylindrical, about as wide as flagellum; (H) oblique frontal ridge absent; (I) protarsal brush weakly developed, on basal two tarsomeres only; (J) front femur not modified (*middle and hind femora extremely robust, with distinct subtriangular processes flanking the articulation with the tibia*); (K) base of hind femur without any specially modified setae; (L) subgenital brush inconspicuous, composed of very short, simple, semirecumbent setae; (M) apex of S6 moderately produced medially, broadly rounded; (N) no conspicuous subapical fringe of setae on sterna (there is a very sparse fringe of weakly plumose, recumbent setae); (O) pygidial plate subtruncate apically; (P) S7 not specially modified, disc subtriangular, tapering to a distinctly truncate apical margin; (Q,R,S) median process of S8 long, narrow, parallel-sided except for slightly widened apex, bearing stiff, narrow, sharply pointed spinose setae; median process lying in same plane as base of sternum; (T) gonostylus long, narrow, circular in cross section, *with transverse ridge at base dorsally, bearing a sparse fringe of long, simple setae* (Figure 128, arrow); (U) inner basal shelf of gonostylus present, bearing a dense cluster of very short, thick, heavily melanized setae (Figure 127); (V) vestiture of gonostylus composed of very short, simple setae, less than half as long as gonostylus (the setae arising from the transverse dorsal ridge are much longer, almost as long as the gonostylus, Figures 127, 128); (W) no basoventral lobe on gonostylus; (X) cluster of a few simple setae, about one-third as long as gonostylus, in a more or less transverse linear arrangement, at ventral base of gonostylus (Figure 127); (Y) gonobase not reduced in size; (Z) *ventral hook present on penis valves, mesally directed, not apparent in lateral view* (Figures 127, arrow, 128); (AA) *inner ridge present on penis valves,*



Figs. 121-129: Male genitalia of *vincta* group (Figs. 121 - 126) and *odontophora* group (Figs. 127 - 129). **Fig. 121.** Genital capsule, dorsal view, *N. zebrata*; **Fig. 122**. Same, ventral view. Arrow shows ventral hook on penis valve; **Fig. 123.** Gonostylus and penis valve of *N. zebrata*, lateral view. Arrow shows ventral hook on penis valve; **Fig. 124.** Right penis valve, dorsal view, *N. suffossa.* Arrow indicates ridge on inner face of valve; **Fig. 125.** Same, *N. besseyi*; **Fig. 126.** Same, *N. aztecorum*; **Fig. 127**. Genital capsule, ventral view, *N. argentea.* Arrow indicates ventral hook on penis valve; **Fig. 128**. Same, lateral view. Arrow indicates transverse dorsal ridge on gonostylus; **Fig. 129.** Right penis valve, dorsal view, *N. argentea.* Arrow indicates ridge on inner face of penis valve. Scale bar = 0.5 mm for Figs. 121 - 123, 127 - 128; = 0.25 mm for Figs. 124 - 126, 129.

with a very distinct toothlike projection at base of ridge (Figure 129, arrow); (BB) *outer lateral ridge present on penis valves, carinate in middle portion, fading out anteriorly and posteriorly*; (CC) penis valves not dorsally flattened; (DD) no basoventral swelling on penis valves; (EE) apex of penis valves acute; (FF,GG) invagination of dorsal gonocoxite distinct, narrow; inner lobe of gonocoxite broad, subtriangular, broadly rounded apically.

COMMENTS: This small Old World group is phenetically very distinctive. Schwarz's (1966) paper contains a thorough description of its numerous striking autapomorphies, which led him to name it as a new genus, *Acanthonomada*. The phylogenetic position of this group has already been discussed in the preceding description of its putative sister taxon, the *vincta* group.

BIOLOGY: No detailed biological studies have been published for the species in this group. Schwarz (1966) suspected that the host of *Nomada argentea* is *Andrena cubiceps* Friese, since all six specimens of the parasite that he collected for his type series were taken in an isolated nest aggregation of that species of *Andrena*.

vegana group

Cephen Robertson, 1903. Canadian Entomol. 35: 174, 176. Type species: *Nomada texana* Cresson, 1872; original designation and monobasic.

Hypochrotaenia subgenus *Aphelonomada* Snelling, 1986. Contrib. Sci. Los Angeles Co. Nat. Hist. Mus. 376: 9-13. Type species: *Nomada cruralis* Moure, 1960; original designation and monobasic.

Hypochrotaenia Holmberg, 1886. An. Soc. Cient. Argentina 22: 273. Type species: *Hypochrotaenia parvula* Holmberg, 1886; original designation and monobasic.

Nomada subgenus *Micronomada* Cockerell & Atkins, 1902. Ann. Mag. Nat. Hist. (7)10: 44. Type species: *Nomada modesta* Cresson, 1863; original designation.

Nomadosoma Rohwer, 1911. Entomol. News 22: 24. Type species: *Pasites pilipes* Cresson, 1865; original designation and monobasic.

Polybiapis Cockerell, 1916. Entomol. News 27: 208. Type species: *Polybiapis mimus* Cockerell, 1916; original designation.

DESCRIPTION: (a) labrum L/W < 1 (except in *tibialis*); (b) apex of mandible simple, narrowly rounded or subacute; (c) relative length of first two flagellomeres variable, but first usually longer than second; (d) preoccipital ridge almost always smoothly rounded throughout, but angulate ventrally in *limata*, angulate dorsally in one undescribed species; (e) *postocciput between posterior tentorial pits distinctly and abruptly recessed below level of postgenal bridge* (this character is most evident in neotropical forms, as shown in Figure 30, and weakly expressed in some North American species, such as *melanoptera*, *vegana*, and *fervida*, as shown in Figure 31); (f) base of proboscideal fossa narrowly constricted (Figures 30, 31); (g) malar space closed posteriorly; (h,i) pronotal collar variable, ranging from sharply carinate with anteriorly projecting lateral angles, to very broadly rounded with lateral angles subhemispherical and "swollen"; (j) *lateral ridge of pronotum distinct, strongly angulate or carinate, sometimes extending upward to join lateral angle of pronotal collar* (Figures 36, 37, **lr**; lateral ridge rather weak in one undescribed species); (k) anterior margin of pronotum usually sharply angulate in profile (broadly rounded or very weakly angulate in two undescribed species); (l) *distinct cuticular flange on neck of pronotum* (Figure 36, **fl**); (m) metapleuron variable, usually flat or gently convex throughout, but occasionally distinctly protuberant above; (n) ridge above propodeal spiracle variable, usually indistinct when present (sometimes distinct in *limata*); (o) scutellum variable, with or without distinct posterior face; (p) *sculpturing of propodeal enclosure uniformly granulose or shagreened, or with very fine rugulae in a fingerprint pattern*; (q) no ridge or carina marking lateral margin of propodeal enclosure; (r) procoxal spine variable, but usually present (absent in *advena*, *pilipes*, *simplicicoxa* (has a spinose process in a different position on the procoxa), *tibialis*, and five undescribed species); (s) lateral carina on procoxa variable, with complete carina present in many neotropical species; (t,u) sculpturing of metasomal terga variable, ranging from closely and distinctly punctate with very narrow impunctate apical margin, to weak, widely spaced punctures with a broad impunctate apical margin; (v) vein 1st r-m of forewing usually present (absent in *mimus*, *parvula*, *pilipes*, *polybioides*, sometimes in *panamensis* and *trapidoi*); (w) vein Rs complete; (x) apex of marginal cell broadly rounded; (y) no unusual modifications of propodeal vestiture. **Females**: (A) *paraocular ridge absent* (Figure 51); (B) setae on outer face of hind tibia variable, *with spinose setae present in many neotropical species*; (C) setae of pseudopygidium basically of typical *Nomada* form, although they appear to be either longer and narrower, or less densely overlapping, than in other *Nomada*; (D) pygidial plate variable, with apex narrowly rounded, very broadly rounded, or intermediate; (E) distal setae of hind tibia variable, usually with a few straight, spinose setae as in most other *Nomada* (but *fervida* has a dense cluster of many flattened, slightly curved setae). **Males**: (F) *anterior articulation of mandible with very strongly recurved flange or flattened, disc-shaped structure* (Figure 24, arrow); (G) scape cylindrical, about as wide as flagellum or slightly wider, never greatly enlarged; (H) oblique frontal ridge absent; (I) protarsal brush variable, often weak, absent in *costalis* and one undescribed species; (J) front femur not greatly enlarged; (K) base of hind femur unmodified, without flocculus; (L) *subgenital brush with setae long, erect, often recurved apically* (brush reduced to a narrow, longitudinal median strip of erect setae on sterna 6, 5, and sometimes 4, as in Figure 7d, in *melanoptera*, *putnami*, *tiftonensis*, *texana*, and three undescribed species); (M) apex of S6 moderately produced mesally,

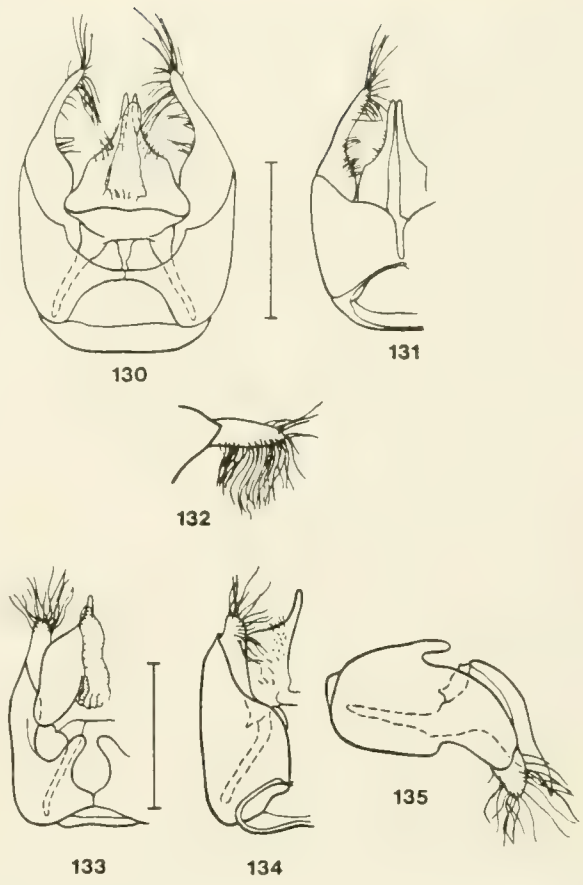


Fig. 130. Genital capsule, dorsal view, *Nomada articulata* (*erigeronis* group). **Fig. 131.** Same, ventral view; **Fig. 132.** Lateral view of gonostylus, *N. crotchii* (*erigeronis* group); **Fig. 133.** Genital capsule, dorsal view, *N. vegana* (*vegana* group); **Fig. 134.** Same, ventral view; **Fig. 135.** Same, lateral view. Scale line = 0.5 mm.

broadly rounded; (N) no subapical fringe of setae on metasomal sterna (entire surface of sterna uniformly covered with long, recumbent setae in many neotropical species); (O) apex of pygidial plate varies from distinctly notched to broadly rounded; (P) S7 not specially modified; evenly rounded on apical margin; (Q,R,S) median process of S8 short to moderately long, dorsoventrally compressed, tapering from base to narrowly rounded apex, with spinose setae (apical pair usually stout and rather clawlike), usually distinctly angulate in profile (weakly angulate or flat in profile in *gutierreziae* and three undescribed species); (T) gonostylus cylindrical, usually narrow and much longer than wide, but very short and broad in *putnami*, *tibialis*, and two undescribed species, and fairly broad (*i.e.* very similar to species in the *ruficornis* group) in *pallidelutea*, *vegana*, and *suavis*; (U) no inner basal shelf on gonostylus; (V) vestiture of gonostylus sparse, setae simple, more than half as long as gonostylus; (W) no basoventral lobe on gonostylus; (X) no setal tuft at ventral base of gonostylus; (Y) *gonobase greatly reduced, not projecting beyond base of gonocoxites in lateral view* (Figures 133-135); (Z) no ventral hook on penis valves; (AA) no inner ridge on penis valves; (BB) *lateral ridge on penis valves distinctly carinate, penis valve triangular in cross section* (also in the *erigeronis* and *roberjeotiana* groups); (CC) *penis valve with a flattened surface at right angle to longitudinal axis of genital capsule* (shown most clearly in Figure 92); (DD) no basoventral swelling on penis valve; (EE) apex of penis valve acute or narrowly rounded; (FF,GG) invagination of dorsal gonocoxite distinct, *inner lobe usually narrow and digitiform* (Figure 133), but shorter and broader (i.e. same as in *ruficornis* group) in *pallidelutea*, *suavis* and *vierecki*. Even in the latter species, *the outer arm of the gonocoxite (the portion laterad of the dorsal invagination) is long and narrow, extending far beyond the invagination, and thus easily distinguished from all other* Nomada.

COMMENTS: This is one of the most phenetically distinct groups within *Nomada*. Snelling (1986) proposed recognizing it as a separate genus, *Hypochrotaenia*, with three subgenera: *Hypochrotaenia* s. str., *Micronomada*, and *Aphelonomada*. My reasons for keeping this group within *Nomada* are discussed in the section on the monophyly of *Nomada* and in the cladistic analyses. *Micronomada* is defined only by the absence of apomorphic characters that are diagnostic of Snelling's other two subgroups, although some species within *Micronomada* share characters that are clearly apomorphic, such as the swollen pronotal collar and the unusual subgenital brush of *putnami* and allied species. A detailed cladistic analysis of the entire *vegana* group is desirable, but beyond the scope of the present study.

The *vegana* group is restricted to the New World, and all of the neotropical material I have seen (extending as far south as Argentina) belongs to this group. It is also fairly common in North America, especially in the West, where it is represented by the relatively plesiotypic species that have traditionally been treated as the subgenus *Micronomada*. The affinities of *Micronomada* with the neotropical species have long been recognized (e.g. Cockerell, 1911).

Snelling (1986) listed 68 species names that he assigned to his genus *Hypochrotaenia*. He did not attempt to identify synonyms in this list, and he is presently working on the species-level taxonomy of this group. He has identified at least 17 undescribed species in the material he has assembled for study (personal communication).

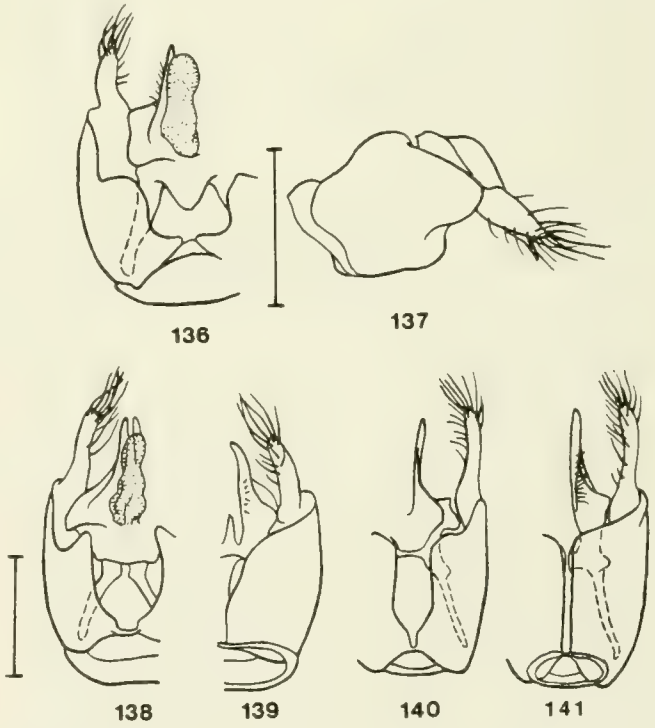
BIOLOGY: Known hosts for the *vegana* group are summarized in Alexander (1991). Most neotropical species for which published data are available (*cubensis*, *pilipes*, and *?tomentifera*) are parasites of *Exomalopsis* species, although Eickwort (1988) has taken *Nomada krugii* (including immature stages) from nests of *Agapostemon* (Halictidae) in the West Indies (Hispaniola). Four North American species (*formula*, *gutierreziae*, *suavis*, and an undetermined species) parasitize *Exomalopsis* (Anthophoridae) or halictids (*Agapostemon* and *Nomia*). There is no current evidence that species of the *vegana* group parasitize *Andrena*.

roberjeotiana group
(paraphyletic)

Nomadita Mocsáry, 1894. Termes. Fuzetek 17: 37. Type species: *Nomadita montana* Mocsáry, 1894; monobasic.

Nomada subgenus *Callinomada* Rodeck, 1945. Entomol. News 56: 181. Type species: *Nomada antonita* Cockerell, 1909; original designation.

DESCRIPTION: (a) Labrum L/W < 1; (b) mandible usually simple, apex narrowly rounded (apex very broadly rounded in *abyssinica*, bifid in *guichardiana*); (c) relative length of first two flagellomeres variable: usually the two are about equal or the first is longer than the second; (d) preoccipital ridge usually angulate or carinate (very weakly angulate in *cleopatra*, evenly rounded in *elegantula* and *melanosoma*); (e) postocciput not distinctly recessed below level of postgenal bridge (slightly recessed in *arasiana* and *galloisi*); (f) base of proboscideal fossa rounded; (g) malar space closed posteriorly (narrowly open in some males); (h) mesal portion of pronotal collar carinate or angulate, *usually distinctly indented* (indentation weak or absent in *abyssinica*, *africana*, *cleopatra*, *eximia*, *guichardiana*, *hararensis*, *obtusifrons*, *placida*, *roberjeotiana*, and *timberlakei*), compressed against strongly arched anterior margin of scutum in *elegantula* and *melanosoma* (this condition also commonly occurs in the *furva* group); (i) lateral portion of pronotal collar rounded when viewed from in front, angulate or carinate along crest of curve, sometimes projecting slightly forward; (j) lat-



Figs. 136-141: Male genitalia in the *roberjeotiana* group: **Fig. 136**. Genital capsule, dorsal view, *Nomada rufipes;* **Fig. 137.** Same, lateral view; **Fig. 138.** Genital capsule, dorsal view, *N. elegantula* ; **Fig. 139.** Same, ventral view; **Fig. 140**. Genital capsule, dorsal view, BMNH specimen from Ethiopia tentatively identified as *N. hararensis* . Freehand drawing; **Fig. 141**. Same, ventral view. Scale bar = 0.5 mm for Figs. 136, 137; = 0.25 mm for Figs. 138, 139.

eral ridge of pronotum usually sharp and distinct, but occasionally broadly rounded (very weak or absent in *elegantula* and *melanosoma*); (k) anterior margin of pronotum variable; usually angulate, sometimes very distinctly so, but angulation weak or absent in *cleopatra*, *ecarinata*, *elegantula*, *melanosoma*, *sarta*, and *timberlakei*; (l) no distinct flange on neck of pronotum; (m) metapleuron not protuberant above; (n) ridge above propodeal spiracle present or absent; (o) scutellum variable, usually with distinct dorsal and posterior faces, but evenly convex in profile in some species, e.g. *cleopatra*, *elegantula*, *errans* and *melanosoma*; (p) sculpturing of propodeal enclosure usually finely shagreened throughout, or with very fine rugulae arranged in a fingerprint pattern (rugose basally, granulose or shagreened apically in *elegantula*, *melanosoma*, and most Afrotropical species: *abyssinica*, *africana*, *guichardiana*, and *hararensis*, not recorded for *aethiopica*, *cordillera*, and *eximia*); (q) lateral margin of propodeal enclosure not marked by a disinct ridge or carina; (r) procoxa with or without spinose process, which varies in prominence when present; (s) no carina on outer face of procoxa; (t,u) sculpturing of metasomal terga varies from closely and distinctly punctate with very narrow impunctate apical margin, to sparsely and finely punctate with wide impunctate apical margin; (v) vein 1st r-m of forewing usually present, but absent in *koikensis* (and in occasional individuals of other species); (w) vein Rs of forewing complete; (x) apex of marginal cell pointed or narrowly rounded, in contact with costal margin of wing; (y) *vestiture generally very short and sparse, often virtually absent from propodeum* (consistently longer in males than females, fairly long in both sexes of *waltoni* from the Himalayas, *kusdasi* from Turkey and Israel, and in Afrotropical species; dense patches of long, thickly plumose, white setae on mesepisternum and lateral angles of propodeum in *elegantula* and *melanosoma*). **Females**: (A) paraocular ridge present (sometimes weak in *okamotonis*); (B) female without spinose setae on outer face of hind tibia; (C) pseudopygidium of typical *Nomada* form; (D) pygidial plate tapering from base to a narrowly rounded apex; (E) distal setae of hind tibia typically short, stout, spinose, not unusually modified (flattened, apically expanded and bluntly rounded, arranged in a closely packed linear array with anywhere from 2 or 3 to 15 or 20 setae in *elegantula* and four undescribed species). **Males**: (F) anterior articulation of mandible with a very distinct flange, often almost disclike as in *vegana* group; (G) scape cylindrical, not conspicuously enlarged, but wider than flagellum in *issikii* and *guichardiana*; (H) no oblique frontal ridge; (I) protarsal brush present, usually very conspicuous (first one or two tarsomeres conspicuously swollen in *abyssinica* and [according to description in Eardley and Schwarz, 1991] *guichardiana*); (J) front femur not conspicuously enlarged or flattened; (K) base of hind femur unmodified, without flocculus; (L) subgenital brush variable: setae long, erect, apically curved in *abyssinica*, *africana*, *arasiana*, *errans*, *elegantula*, *eximia*, *galloisi*, *guichardiana*, *hararensis*, *melanosoma*, *okamotonis*, *roberjeotiana*, and *waltoni*; very short and simple, semirecumbent in other species; (M) apex of S6 moderately produced mesally, apex of projection broadly rounded; (N) subapical setal fringe on metasomal sterna usually absent, but present in *melanosoma* and several Afrotropical species (*abyssinica*, *africana*, *eximia* [according to description in Eardley & Schwarz, 1991], and *guichardiana*); (O) apex of pygidial plate rounded or weakly emarginate (may vary *within* species); (P) S7 not specially modified, apical margin evenly rounded; (Q,R,S) *median process of S8 dorsoventrally compressed, short and broad, tapering from base to broadly rounded apex, angulate or straight in profile, process bearing very robust, clawlike setae* (this state also occurs in the *erigeronis* group, and the South African species *whiteheadi* has the median process relatively long and narrow, as in the *vegana* group); (T) gonostylus cylindrical, long and narrow (somewhat flattened and apically truncate in *waltoni*); (U) no inner basal shelf on gonostylus; (V) vestiture of gonostylus long (setae more than half as long as gonostylus), sparse, simple; (W) no basoventral lobe on gonostylus; (X) no basoventral setal tuft on gonostylus (except for a sparse tuft of short, simple setae in *whiteheadi*); (Y) *gonobase reduced in size, but not as greatly reduced as in* vegana *group, clearly visible in lateral view of genital capsule* (Figure 136, 137) [One Ethiopian specimen from BMNH, shown in Figures 140-141 and matching *hararensis* in overall appearance, has a gonobase as greatly reduced as in members of the *vegana* group.]; (Z) no ventral hook on penis valve; (AA) no ridge on inner face of penis valve; (BB) *outer face of penis valve with a sharp, distinctly carinate lateral ridge, penis valve roughly triangular in cross section* (Figure 95, **or**); (CC) penis valve not dorsally flattened; (DD) no basoventral swelling on penis valve; (EE) apex of penis valve acute; (FF,GG) *invagination of dorsal gonocoxite variable, usually weak but discernible, but virtually absent in* aquilarum, obtusifrons, snowii, *and* galloisi*; inner dorsal lobe generally short and inconspicuous* (distinct invagination and inner lobe in *elegantula* and *melanosoma*, Figure 138).

COMMENTS: This is a heterogeneous group whose monophyly is doubtful. Authors dating back at least to Perkins (1919) have remarked upon the distinctive form of male S8 in this group, although Snelling (1986) was apparently the first to point out that this character is similar in other groups (he commented on the similarity between the *roberjeotiana* and *vegana* groups, but his illustrations show that S8 is at least as similar in the *erigeronis* and *roberjeotiana* groups). As discussed in the cladistic analysis, the correct phylogenetic interpretation of this similarity (and of similarities in the genitalia, subgenital brush, and procoxal structure) is not entirely clear. Although the *vegana* group can readily be characterized by diagnostic features that are almost certainly apomorphic, it consistently clusters in my cladistic analyses with three other groups, *roberjeotiana*, *abyssinica*, and *elegantula*, that are not so distinctive and that share character states that are apparently plesiomorphic with respect to corresponding states in the *vegana* group. Many of these same character states (most notably the form of S8 and the outer lateral ridge on the penis valves) also occur in the *erigeronis* group. Pending a more detailed study of this unresolved polytomy, I will recognize the phenetically distinct and monophyletic *vegana* and *erigeronis* groups, and assign the remaining species to the probably paraphyletic *roberjeotiana* group.

The *roberjeotiana* group in this sense corresponds closely to the taxon *Nomadita*, originally described as a genus by Mocsáry (1894) but now most commonly treated as a subgenus of *Nomada* (e.g. by Snelling, 1986; Broemeling, 1988; and Schwarz 1986, 1989). The following species assignments are new:

Nomada xanthophila Cockerell, 1900; known only from a single male specimen from New Mexico, U.S. Cockerell (1900, 1903c), considered it to belong to either *Xanthidium* or *Holonomada* (his original description compares it to *Nomada superba*), and Snelling (1986) placed it (as "*xanthophilus* Cockerell 1900") in his subgenus *Nomada*. However, the genitalia and S8, subgenital brush, sculpturing of the propodeal enclosure, extremely short and sparse vestiture of the propodeum, and sharply carinate pronotal collar with a distinct median indentation all indicate that it belongs in the *roberjeotiana* group.

Nomada kusdasi Schwarz, 1981; from Turkey and Israel. Schwarz emphasized similarities between *kusdasi* and *glaberrima*, an aberrant member of the *integra* group (see comments on that group). The two species are similar in overall appearance, most notably in the rather weak, somewhat shiny integumental sculpturing and general coloration. However, the genitalia and associated sterna indicate that these two species are not closely related, and support the placement of *kusdasi* in the *roberjeotiana* group.

The major sense in which my concept of the *roberjeotiana* group differs from the subgenus *Nomadita* of most authors is that it in-

cludes a small group of North American species that have not previously been assigned to *Nomadita* and do not resemble other members of this group in overall appearance. These are the species treated as the "*elegantula* group" in the cladistic analyses. This group contains only three named species, *elegantula* , *marginella*, and *melanosoma*. The anomalous nature of these species was first pointed out to me by Roy Snelling (personal communication), who included them in the subgenus *Nomada* in his 1986 paper. He has identified an additional ten undescribed species that he would assign to this group. Six of these ten undescribed species, as well as *marginella*, are known only from females. Although in overall appearance the species of this group resemble small *Nomada* sensu Snelling, the male terminalia clearly exclude *elegantula* and *melanosoma* (and the four undescribed species whose males are known) from Snelling's *Nomada*.

Broemeling (1988) called attention to four species, *olhae, jasnitskii, scheviakovi*, and *belikovi*, that Cockerell (1928) described from Siberia and considered to be closely related to *roberjeotiana*. Schwarz (1988) has recently examined the types of all four species and concluded that they are junior synonyms of well-known European species, none of which are in the *roberjeotiana* group.

Snelling and Broemeling have noted that most members of the *roberjeotiana* group share a distinctive vestiture, which is extremely sparse and short, or absent altogether, especially on the propodeum. However, the Himalayan species *waltoni* has fairly long, dense vestiture on the propodeum. This species clearly belongs in the *roberjeotiana* group because, in addition to the major diagnostic features listed in the description of the group, it shares a distinctive apomorphic modification of the interantennal area that I have found only in certain Palearctic species in this group. Most of the Afrotropical species of the *roberjeotiana* group also have relatively long vestiture, as does *kusdasi* from Israel and Turkey.

The center of diversity of the *roberjeotiana* group appears to be in central Asia (M. Schwarz, personal communication), a region that has not been well collected. A hint of the diversity of this group in eastern Asia may be gained from its relative richness, in both species and individuals, in the fauna of Japan. A collection of undetermined material from the Institute of Biology and Pedology in Vladivostok, Russia, kindly loaned to me by N.V. Kurzenko, also contains several species and many individuals that belong in this group. Although the species diversity declines outside of Asia, the group extends across Europe to the British Isles, and into North America, with seven species (including *elegantula* and *melanosoma*) in the western and central regions of the U.S., and only one with a distribution primarily east of the Mississippi River (Broemeling, 1988).

BIOLOGY: The temperate zone species of this subgroup are typically active in late summer, but *waltoni* (collected at 3900 m. in the Himalayas) was taken in June, and North African specimens have been collected in March and April. Tsuneki (1986) recently described a new species, *etigonis*, that he considered closely related to *arasiana* and *galloisi*, both of which I have examined and determined to belong in the *roberjeotiana* subgroup. *Nomada etigonis* is active in late spring (May and June) in Japan, an observation which Tsuneki noted as unusual when describing the species.

No reliable host records are available for North American or Japanese species of this group, although Snelling (1986) suggested that the North American species might parasitize *Andrena* (*Cnemiandrena*). Host records from the older European literature, such as those listed in Schmiedeknecht (1882), must be interpreted cautiously, since they were often based on casual associations and not on careful field studies (Perkins, 1919). Even Perkins seems to have based his associations on repeated observations of parasites seen together with their putative hosts, rather than on the more conclusive evidence of rearing parasites taken from nests whose hosts are accurately determined. Hence, reports of *N. rufipes* as a parasite of various species of *Halictus* and *Colletes* require verification, and until proven otherwise it is safest to assume that the familiar European species *rufipes, roberjeotiana*, and *obtusifrons* are parasites of *Andrena*. Perkins (1919) considered it noteworthy that the species of *Andrena* commonly parasitized by *rufipes* are not closely related to the *Andrena* hosts of *obtusifrons* and *roberjeotiana* (although Perkins' evidence for his hypotheses of relationship within *Andrena* is not explicitly presented). Host associations that Perkins considered well documented for British species of the *roberjeotiana* subgroup are as follows: *Nomada rufipes* on *Andrena fuscipes* and *A. denticulata*; *Nomada roberjeotiana* (as *tormentillae*) on *Andrena tarsata*; *Nomada obtusifrons* on *Andrena coitana* and perhaps on *Andrena tarsata*. Stoeckhert (1932) reported on his own observations of *Nomada* species in southern Germany, as well as published reports of other continental European workers. The *Andrena* hosts reported by Perkins in Britain were also the associations Stoeckhert considered best substantiated in Europe. He suggested *Andrena nitidiuscula* and *A. pallitarsus* as possible hosts for *Nomada errans*.

erigeronis group

Centrias Robertson, 1903. Canadian Entomol. 35: 174, 176. Type species: *Nomada erigeronis* Robertson, 1897; original designation.

Nomada subgenus *Nomadula* Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 611. Type species: *Nomada articulata* F. Smith, 1854; original designation.

DESCRIPTION: (a) Labrum L/W < 1; (b) mandible simple, apex narrowly rounded; (c) first flagellomere shorter than second, *first flagellomere very short in male* (the first flagellomere is also very short in many males of the *ruficornis* group); (d) preoccipital ridge usually distinctly carinate, but angulate in *crotchii*; (e) postocciput not distinctly recessed below level of postgenal bridge; (f) base of proboscideal fossa rounded; (g) malar space closed posteriorly (narrowly open in some males); (h) median portion of pronotal collar usually carinate, often with a distinct median notch (angulate in *crotchii, rohweri*, and four undescribed species); (i) lateral portion of pronotal collar rounded when viewed from in front, but angulate or carinate along crest of the curve; (j) lateral ridge of pronotum distinct, but rounded or weakly angulate; (k) anterior margin of pronotum usually rounded or weakly angulate in profile, more distinctly angulate in *scitiformis, rohweri*, and one undescribed species; (l) no distinct flange on neck of pronotum; (m) *metapleuron distinctly protuberant above, or with a distinct longitudinal carina* (Figure 38, **mtpl**; weak or absent in *seneciophila*); (n) ridge over propodeal spiracle often weak or absent, but *rubicunda* consistently has a distinct ridge; (o) scutellum nearly right-angled in profile, with distinct dorsal and posterior faces, often bilobed; (p) propodeal enclosure rugose or reticulate basally, granulose or shagreened apically; (q) lateral margin of propodeal enclosure not marked by a disinct ridge or carina; (r) *procoxal spine present* (short and inconspicuous in *crotchii, semiscita*, and *seneciophila*); (s) no carina on outer face of procoxa; (t) sculpturing of metasomal terga variable, most frequently consisting of distinct, rather fine, closely spaced punctures, but punctures are coarse, dense (one to two puncture diameters apart), with integument polished between punctures, in *erigeronis, scitiformis*, and *semiscita*; (u) apical impunctate margin of metasomal terga very narrow except in *rohweri* and two undescribed species; (v,w) forewing with three submarginal cells; (x) apex of marginal cell pointed or narrowly rounded, in contact with costal margin of wing; (y) vestiture variable, but with no striking apomorphic states. **Females**: (A) paraocular ridge present; (B) female without spinose setae on outer face of hind tibia; (C) pseudopygidium of typical *Nomada* form; (D) pygidial plate tapering

from base to a narrowly rounded apex; (E) distal setae of hind tibia typically short, stout, spinose, not unusually modified. **Males**: (F) anterior articulation of mandible usually with a weak but discernible flange, but this flange is very weak or absent in *crotchii* and *rohweri*; (G) *scape cylindrical, distinctly enlarged, much wider than flagellum, completely enclosing pedicel* (although always present in the *erigeronis* group, this state also occurs in many species of the *ruficornis* group); (H) no oblique frontal ridge; (I) protarsal brush usually present, but absent in *crotchii* and *rohweri*; (J) front femur not conspicuously enlarged or flattened; (K) base of hind femur never bearing a flocculus, but distinctly concave in *articulata, australis,* and *erigeronis*; (L) *subgenital brush very distinctive, with long, erect, flexible setae that are arranged in a single median and two lateral tufts in all species except* crotchii, rohweri, *and four undescribed species* (Figures 7e,f); (M) *apex of S6 broadly truncate, not produced medially* (Figure 7f); (N) *metasomal sterna always with a distinct subapical setal fringe, setae erect and relatively sparse in* crotchii (Figure 7e), rohweri, *and four undescribed species, recumbent and very dense in other species (e.g.* articulata, *Figures 7f, 69)*; (O) pygidial plate emarginate or distinctly notched apically (except in one undescribed species); (P) S7 not specially modified, apical margin evenly rounded; (Q,R,S) *median process of S8 dorsoventrally compressed, short and broad, tapering from base to broadly rounded apex, angulate or straight in profile, process bearing very robust, clawlike setae* (this same state occurs in the *roberjeotiana* group); (T) *gonostylus cylindrical, usually long and narrow apically, distinctly widened basally* (Figures 130, 131) [diameter uniform throughout and gonostylus rather broad in *crotchii* (Figure 132), more like the state found in most species of the *ruficornis* group]; (U) no inner basal shelf on gonostylus; (V) vestiture of gonostylus more than half as long as gonostylus, rather sparse, simple, *arising only from apex and ventral face of gonostylus, absent from dorsal face* (Figures 130-132); (W) no basoventral lobe on gonostylus; (X) no basoventral setal tuft on gonostylus, *but broadened basal area often has a few short, simple setae* (Figure 131); (Y) *gonobase reduced in size, but not as greatly reduced as in* vegana *group, clearly visible in lateral view of genital capsule*; (Z) no ventral hook on penis valve; (AA) no ridge on inner face of penis valve; (BB) *outer face of penis valve with a sharp, distinctly carinate lateral ridge, penis valve roughly triangular in cross section (Figure 94)* [this state also occurs in the *vegana* and *roberjeotiana* groups]; (CC) penis valve not dorsally flattened; (DD) no basoventral swelling on penis valve; (EE) apex of penis valve acute; (FF,GG) *no invagination or inner lobe on dorsal gonocoxite* (Figure 130). (On several species, there is a flange at a right angle to the plane of the gonocoxite in the position where the inner lobe would be found in groups that have an inner lobe, so perhaps it would be more accurate to say that the inner lobe is reoriented rather than absent.)

COMMENTS: The males of this group are very distinctive, with their elaborate subgenital brushes, antennae with enlarged scapes, very short first flagellomeres, and more distal flagellomeres typically bearing spinose processes and distinct concavities on the posterior (dorsal) side, in addition to the genitalic characters indicated in the preceding description. Females can usually be distinguished from other *Nomada* by a combination of rather subtle features (spinose procoxae, protuberance on metapleuron, short first flagellomere). Snelling (1986) considered these traits to be distinct and consistent enough to warrant recognizing this group as a genus, *Centrias*, which he regarded as intermediate between his genera *Hypochrotaenia* and *Nomada*. The cladistic analyses presented here indicate that the *erigeronis* group may (or may not) be part of a complex including the *roberjeotiana* and *vegana* groups. The *erigeronis* group is restricted to North America, with the greatest number of species in the west. Most of the species that Snelling included in his genus *Centrias* belong to a monophyletic assemblage in which the males have a very distinctive, clearly apomorphic three-tufted subgenital brush (Figure 7f) and vestiture of very dense, appressed setae on metasomal sterna 4 and 5 (Figures 7f, 69). The species in this assemblage are *articulata, australis, erigeronis, friesiana, pascoensis, rubicunda, scita, sciliformis, semiscita, seneciophila,* and *sophiarum*. Although this assemblage is easily characterized and there is strong evidence for its monophyly, there are a few species in Snelling's *Centrias* that have the characteristic genitalic features of the other species, but lack the three-tufted subgenital brush and sternal setal fringe.

Two species originally described by Cockerell, *frankei* and *jennei*, have long been regarded as closely related to *pascoensis* in the *erigeronis* group, because Cockerell said they were when he described them. I have dissected the holotypes of both of these species (both are male), and neither of them is at all close to *pascoensis* in genitalic characters. Both clearly belong in the *ruficornis* group, and their presumed affinity to *pascoensis* is superficial.

BIOLOGY: Although a few species in this group, especially *articulata* and *crotchii*, are relatively common in collections, little has been published about their biology. Snelling (1986, Table 1) lists the following host associations: *Agapostemon sericeus* (listed by Snelling as *radiatus*) and *A. virescens* (Halictidae) for *Nomada articulata*, and *Andrena prunorum* (Andrenidae) for *Nomada crotchii*. On the same Cornell University campus where Eickwort and Abrams (1980) reared *Nomada articulata* from nests of two species of the halictid *Agapostemon*, I found *N. articulata* consistently patrolling an aggregation of *Andrena alleghaniensis* for three consecutive years. I frequently saw marked individuals of *Nomada articulata* enter *Andrena alleghaniensis* nests. However, excavation of scores of nests (over 100 cells uncovered) revealed extremely low rates of parasitism (1 to 2%) and no parasite larvae reared to adulthood for positive identification.

Nomada rodecki Mitchell

This problematic species is known only from a single male specimen in the USNM collection (holotype No. 75223). Although Mitchell (1962) provides a detailed description, I include a redescription here for ease of comparison with my descriptions of other groups. In my description, characters that I could not adequately see on the holotype are noted as "not visible".

DESCRIPTION: (a) labrum L/W < 1; (b) mandible rounded apically; (c) first flagellomere slightly shorter than second; (d) preoccipital ridge carinate; (e) postocciput not visible; (f) base of proboscideal fossa broadly rounded; (g) malar space closed posteriorly; (h) median portion of pronotal collar strongly angulate, almost carinate; (i) lateral angle of pronotal collar rounded when viewed from in front and along the crest of the curve; (j) lateral ridge of pronotum distinct, extending straight up onto neck of pronotum; (k) anterior margin of pronotum evenly rounded in profile; (l) neck of pronotum not visible; (m) metapleuron not protuberant above; (n) distinct horizontal ridge present above propodeal spiracle ; (o) scutellum with dorsal and posterior faces, posterior margin only weakly impressed medially; (p) sculpturing of propodeal enclosure fine, more or less granulose throughout; (q) no distinct ridge marking lateral margin of propodeal enclosure; (r) procoxal spine absent; (s) no lateral carina present on procoxa; (t) punctures on metasomal terga fine but distinct, closely spaced; (u) metasomal terga with narrow impunctate apical margin; (v,w) forewing with three submarginal cells; (x) apex of marginal cell acute or narrowly rounded, contacting costal margin of forewing; (y) vestiture of mesosoma and head extremely short and sparse. **Females**: unknown. **Males**: (F) anterior articulation of mandible with a rather weak flange; (G) scape cylindrical, about as wide as flagellum ; (H) oblique frontal ridge absent; (I) protarsal brush present, but weakly developed; (J) front femur not greatly enlarged or specially modified; (K) no flocculus or basal concavity on hind femur; (L) subgenital brush of very short, sparse setae; (M) apical margin of S6 moderately produced and rounded

mesally; (N) no dense subapical setal fringe on metasomal sterna; (O) apex of pygidial plate obtusely angulate (Figure 104, p. 376 in Mitchell, 1962); (P) S7 damaged; (Q) *median process of S8 laterally compressed, long, narrow, tapering from a broad base to a narrow apex* (Figure 104, p. 376 in Mitchell, 1962); (R) S8 straight, not angulate, in lateral profile; (S) spinose setae on median process of S8 straight, stiff, not extremely stout; (T) gonostylus cylindrical, short, stout, apically rounded, only weakly curved toward midline of genital capsule ; (U) inner basal shelf present on gonostylus, not bearing a dense cluster of specially modified setae; (V) vestiture of gonostylus rather sparse, about as long as gonostylus or longer, apically sinuate or weakly plumose, not distinctly separated into basal and apical tufts (Figure 103, p. 375 in Mitchell, 1962); (W) cylindrical basoventral lobe present on gonostylus; (X) basoventral tuft of long, apically sinuate, weakly plumose setae on gonostylus; (Y) gonobase not distinctly reduced; (Z) no ventral hook on penis valves; (AA) no ridge on inner face of penis valves; (BB) no ridge on outer face of penis valves; (CC) penis valves not dorsally flattened; (DD) no basoventral swelling on penis valves; (EE) apex of penis valves acute; (FF,GG) dorsal face of gonocoxite with shallow invagination and an inner lobe that is very short and broadly rounded.

COMMENTS: When he originally described this species, Mitchell assigned it to the *roberjeotiana* group (as the subgenus *Callinomada*). Snelling (1986) also included it in this group (as the subgenus *Nomadita*), but when Broemeling (1988) revised North American *Nomadita* he removed *rodecki* from this subgenus and placed it in the subgenus *Nomada*, on the basis of characters of the antennae and terminalia. I used it as a terminal taxon in my cladistic analyses because the form of S8 does not exactly conform to the condition found in either the *roberjeotiana* or the *ruficornis* group. The results of my cladistic analysis are in closer accord with Broemeling's conclusion than with that of Mitchell and Snelling.

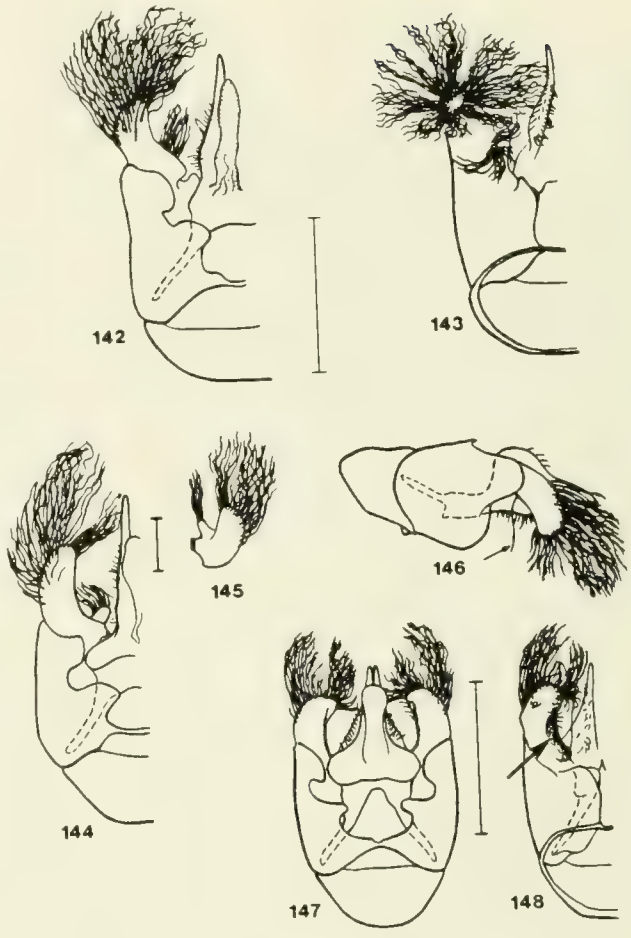
BIOLOGY: The only published information is that the one known specimen was collected in mid-May. Broemeling emphasized that this is "almost two months earlier than any species of [North American] *Nomadita*".

ruficornis group
(paraphyletic?)

Nomada Scopoli, 1770. Annus Historico Naturalis, 4. p. 44. Type species: *Apis ruficornis* Linnaeus, 1758; designated by Curtis (1832).
Gnathias Robertson, 1903. Canadian Entomol. 35: 173, 175-176. Type species: *Nomada bella* Cresson, 1863; original designation.
Nomada subgenus *Heminomada* Cockerell & Atkins, 1902. Ann. Mag. Nat. Hist. (7) 10: 42. Type species: *Nomada obliterata* Cresson, 1863; original designation.
Lamproapis Cameron, 1902. Jour. Bombay Nat. Hist. Soc. 14: 419-420. Type species: *Lamproapis maculipennis* Cameron, 1902; monobasic.
Phor Robertson, 1903. Canadian Entomol. 35: 174. Type species: *Nomada integerrima* Dalla Torre, 1896 (= *Nomada integra* Robertson, 1893; preoccupied); original designation and monobasic.
Xanthidium Robertson, 1903. Canadian Entomol. 35: 174, 177. Type species: *Nomada luteola* Olivier, 1811; original designation.
Includes *zonata* group of Stöckhert, 1941. Mitt. Münchner Entomol. Ges. 31: 1072-1122.

This very large, heterogeneous, and probably paraphyletic assemblage contains the majority of the species within *Nomada*. The species are still very poorly known in large regions where the group is undoubtedly common and diverse, such as North America and eastern Asia. The following group description is based on *Nomada ruficornis*, which is the type species of the genus and is suitable as a "typical" representative of the species group that bears its name (although the mandibles are unusual and apomorphic).

DESCRIPTION: (a) labrum L/W < 1; (b) mandible bifid apically. (This is an apomorphic state in *ruficornis*. Most species in the *ruficornis* group have simple mandibles, although they vary considerably in form, as indicated in Figures 19 - 22. North American



Figs. 142-148: Male genitalia of species of the *ruficornis* and *armata* groups. **Fig. 142.** Genital capsule, dorsal view, *N. banksi*, (*ruficornis* group); **Fig. 143.** Same, ventral view; **Fig. 144.** Genital capsule, dorsal view, *N. luteoloides*, (*ruficornis* group); **Fig. 145.** Right gonostylus of *N. luteoloides*, viewed looking down longitudinal axis of genital capsule; **Fig. 146.** Genital capsule, lateral view, *N. linsenmaieri* (*armata* group). Note that the basoventral setal "tuft" consists of only a single seta, indicated by the arrow; **Fig. 147.** Same, dorsal view; **Fig. 148.** Same, ventral view. Arrow indicates sclerotized patch on inner face of gonostylus. Scale bar = 0.5 mm.

species with bidentate mandibles have long been treated as a subgenus called *Gnathias*.); (c) first flagellomere shorter than second (first very short in male); (d) preoccipital ridge angulate dorsally, becoming rounded lateroventrally (this state varies considerably throughout the group); (e) postocciput not distinctly recessed below level of postgenal bridge; (f) base of proboscideal fossa broadly rounded; (g) malar space closed posteriorly; (h) median portion of pronotal collar angulate; (i) lateral angle of pronotal collar rounded when viewed from in front, but angulate along the crest of the curve; (j) lateral ridge of pronotum rounded, indistinct, extending straight up onto neck of pronotum; (k) anterior margin of pronotum evenly rounded in profile; (l) no distinct flange on neck of pronotum; (m) metapleuron not protuberant above; (n) ridge above propodeal spiracle indistinct or absent (the degree of development of this character varies considerably throughout the *ruficornis* group); (o) scutellum right-angled in profile, with distinct dorsal and posterior faces; (p)

sculpturing of propodeal enclosure rugose-reticulate basally, shagreened apically (this is the most common state in the *ruficornis* group, but other states occur sporadically throughout the group); (q) no distinct ridge marking lateral margin of propodeal enclosure; (r) procoxal spine absent (almost all species in the *ruficornis* group lack a procoxal spine, but a short spine is discernible in a few species, such as *banksi*, Figure 44); (s) no lateral carina present on procoxa; (t) punctures on metasomal terga fine and weak, but closely spaced basally, becoming sparser apically (this state is very common, but not universal, within the *ruficornis* group); (u) metasomal terga with broad impunctate apical margin; (v,w) forewing with three submarginal cells (as in other groups within *Nomada*, occasional individuals or species in the *ruficornis* group have two submarginal cells); (x) apex of marginal cell acute or narrowly rounded, contacting costal margin of forewing; (y) vestiture of mesosoma and head rather sparse, but setae are long and weakly plumose, with no unusual modifications (vestiture is variable within the *ruficornis* group). **Females**: (A) paraocular ridge present; (B) no spinose setae on outer face of hind tibia (there are weak tubercles bearing short, simple, sharply pointed setae. As in other groups, these tubercles tend to be more prominent in larger species.); (C) pseudopygidium of the usual *Nomada* form; (D) pygidial plate tapering from base to a narrowly rounded apex; (E) apex of hind tibia with 4-6 long, narrow, spinose setae that are weakly hooked apically (these setae vary in subtle ways throughout *Nomada*, and are often species-specific characters). **Males**: (F) anterior articulation of mandible with a rather weak flange; (G) scape cylindrical, distinctly wider than flagellum (Width of scape relative to flagellum varies considerably, but the conspicuously widened scape is a common state in the *ruficornis* group. The latter state is also present in the *erigeronis* group.); (H) oblique frontal ridge absent; (I) protarsal brush present, but weakly developed (degree of development varies throughout the group); (J) front femur not greatly enlarged or specially modified; (K) no flocculus or basal concavity on hind femur; (L) *subgenital brush of short, fine, weakly plumose setae that are semirecumbent, directed posterad, dense on apicomedian portion of disc of sternum, not forming an apical or lateral fringe, as in Figure 7b* (the subgenital brush in the *integra*, *armata*, *belfragei*, *superba*, and *basalis* groups is also of this type); (M) apical margin of S6 moderately produced and rounded mesally; (N) no dense subapical setal fringe on metasomal sterna; (O) apex of pygidial plate rounded or weakly emarginate (in many species in the *ruficornis* group, the pygidial plate is deeply notched); (P) S7 broadly rounded apically, not specially modified; (Q) *median process of S8 laterally compressed, long, narrow, parallel-sided basally, slightly widened apically* (as in Figures 80 - 82; the median process of S8 in the *integra*, *armata*, *basalis*, *superba*, *bifasciata*, and *trispinosa* groups is also of this type, and the state in *N. gigas* is similar); (R) S8 straight, not angulate, in lateral profile; (S) spinose setae on median process of S8 straight, stiff, not extremely stout; (T) *gonostylus cylindrical, short, stout, apically rounded, only weakly curved toward midline of genital capsule* (as in Figures 142 - 145); (U) inner basal shelf present on gonostylus, not bearing a dense cluster of specially modified setae (the modified setae are present in many species of the *ruficornis* group, e.g. *luteoloides*, Figures 144, 145); (V) *vestiture of gonostylus dense, about as long as gonostylus or longer, apically sinuate or weakly plumose, not distinctly separated into basal and apical tufts* (as in Figures 86, 142 - 145); (W) cylindrical basoventral lobe present on gonostylus (the prominence of this lobe varies considerably within the *ruficornis* group, and it is absent in many species); (X) *conspicuous basoventral tuft of long, apically sinuate, weakly plumose setae on gonostylus*; (Y) gonobase not distinctly reduced; (Z) no ventral hook on penis valves; (AA) no ridge on inner face of penis valves; (BB) no ridge on outer face of penis valves; (CC) penis valves not dorsally flattened; (DD) no basoventral swelling on penis valves; (EE) apex of penis valves acute; (FF,GG) dorsal face of gonocoxite with distinct invagination and an inner lobe that is subquadrate, with apex truncate or weakly rounded.

COMMENTS: Although the *armata*, *basalis*, *belfragei*, *bifasciata*, *furva*, *superba*, and *trispinosa* groups can be reliably distinguished from the *ruficornis* group, the diagnostic features of the former taxa are probably modifications of the states occurring in the *ruficornis* group. If this is true, the *ruficornis* group is paraphyletic relative to these groups, although all these groups taken together are monophyletic with respect to the rest of *Nomada*.

Numerous other small monophyletic subgroups could also be identified within the *ruficornis* complex, but the majority of species would still remain in a large, heterogeneous paraphyletic assemblage. The choice of groups recognized here is admittedly arbitrary and conservative, and may not be very satisfactory to workers primarily interested in species-level taxonomy and the subtle differences that separate very similar-looking species. For the New World, I have delineated groups that correspond as closely as possible to the monophyletic subgenera from Snelling's (1986) revision. For the Old World, I have tried to identify groups that have already been recognized from the New World, plus exclusively Old World groups that appear to be monophyletic and as distinct as the New World groups. There is clearly a need for much more work on this large and challenging group.

This huge paraphyletic assemblage occurs throughout the Holarctic region, but it is absent from South America, Australia, and most of tropical Asia. The extent of its distribution in sub-Saharan Africa is uncertain. The BMNH has specimens of *chrysopyga*, determined by M. Schwarz, from the Tibesti region of northern Chad. Two recently described species from Ethiopia, *aethiopica* and *aurantifascia*, are known only from females and could prove to belong to the *ruficornis* group when the males are found.

The mountainous regions of northern India have several species in the *ruficornis* subgroup, and a few may extend southward into tropical India, but the *Nomada* fauna of Southeast Asia, the Malay Archipelago, New Guinea, Australia, and the southwestern Pacific seems to be comprised only of species in the *furva* group. Farther north, in Japan and China, the *ruficornis* group is very common. It forms the dominant element of the Japanese *Nomada* fauna, just as it does in northern and central Europe and eastern North America.

A complete listing of all the named species in the *ruficornis* group is a formidable task. Some variable European species have literally dozens of recognized synonyms. This may also prove true in North America when the species are better understood. Many names are currently based on only a single sex, and sexual dimorphism is pronounced in this group.

BIOLOGY: Host records are available for only a small fraction of the species in the *ruficornis* group. For some of the European species reported to have several host species, it is very difficult to know how much of the variability is real and how much is due to misidentifications of the parasite (or host). The majority of known hosts are in *Andrena*. However, Rozen (1966) reared both sexes of a *Nomada* species belonging to the *ruficornis* group from a nest of *Halictus ligatus* in New Jersey. Stoeckhert (1932) reported observations of *N. zonata* entering nests of *Halictus maculatus* in Germany, but he also suggested two *Andrena* species as possible hosts of *N. zonata*. The European species *N. flavopicta* may parasitize melittids (*Melitta* and *Dasypoda*), although the evidence for this is not conclusive (Stoeckhert, 1932). Smith (1876) reported recovering a pair of *N. marshamella* (which he called *N. alternata*) in cells excavated from a nest of *Eucera longicornis*. A complete listing of the host records for species in the *ruficornis* group is presented in Alexander (1991).

armata group

Includes *fuscicornis* group of Schwarz, 1977. Mitt. Münchner Entomol. Ges. 66: 67.

DESCRIPTION: As in *ruficornis* group except as follows: (a) labrum L/W > 1 in *fuscicornis, panurgina* (Figure 18), and an undescribed species, L/W < 1 or = 1 in other species; (c) relative length of first two flagellomeres varies considerably, even within species; (f) base of proboscideal fossa rounded in most species, but constricted by strongly developed hypostomal carina in *fuscicornis, linsenmaieri, merceti, nitida, panurgina, panurginoides, polyacantha, rubricoxa, rufoabdominalis, sicula,* and *similis*; (h) median portion of pronotal collar angulate, or compressed against scutum; (o) scutellum variable, usually evenly convex in profile, but distinctly flattened in *panurgina, rubricoxa,* and an undescribed species, distinctly right-angled in *sicula* and *similis*; (p) sculpturing of propodeal enclosure variable, always rugose or reticulate basally, but may be shagreened or finely rugulose apically (most species), or highly polished (*bispinosa, panurgina* and two undescribed species); (v) vein 1st r-m of forewing present (occasionally absent in *armata,* usually absent in *sicula*); (w) vein Rs of forewing complete except in some individuals of *fuscicornis*; (y) vestiture not unusually modified, but dense patches of thickly plumose, white setae on mesepisternum and propodeum are well developed in *armata, bispinosa,* and two undescribed species. **Females**: (A) paraocular ridge present (but usually a weak angulation rather than a distinct carina in *fuscicornis, linsenmaieri, merceti, nitida, panurgina, panurginoides, polyacantha, rubricoxa, rufoabdominalis, sicula,* and *similis*); (E) apex of hind tibia variable, usually within the range of states found in the *ruficornis* group, but produced, usually with flattened or beveled area, with a dense field of short, stout, straight, slightly flattened setae in *fuscicornis, linsenmaieri, merceti, nitida, panurgina, panurginoides, polyacantha, rubricoxa, rufoabdominalis, sicula,* and *similis* (Figure 54). **Males**: (H) *oblique frontal ridge present* (may be reduced and inconspicuous); (J) front femur variable, either unmodified, or greatly enlarged and concave anteriorly (in *armata, corcyraea, eos, femoralis, sanguinea, nausicaa,* and *transitoria,* see Figures 63, 64); (K) base of femur variable: usually a flocculus (Figure 67) is discernible (very weak in *panurgina, linsenmaieri,* and an undescribed species; state in *bifida* is like "pseudoscopa" of *trispinosa* group, Figure 65); (M) apex of S6 moderately produced, evenly rounded, *usually a rounded, weltlike longitudinal ridge is present apicomedially;* (P) S7 with apodemes moderately long, disc of sternum subtriangular, *apical margin laterally compressed, sometimes also strongly recurved or bearing a ventromedian keel*; (U) no inner basal shelf on gonostylus, but inner face of gonostylus *has a longitudinal sclerotized patch* (Figure 148, very weak in some species); (V) vestiture of gonostylus always long, dense, and apically sinuate or plumose, usually fairly evenly distributed across gonostylus (Figures 146 - 148), but showing strong tendency for differentiation into apical and basal tufts in *merceti, rubricoxa,* and *similis*; (X) basoventral setal tuft present on gonostylus (reduced to only two or three setae, as in Figure 146, in *bispinosa, fuscicornis, immaculata, linsenmaieri, merceti, nitida, panurgina, panurginoides, sicula, similis, unispinosa,* and three undescribed species).

COMMENTS: The salient synapomorphies for this primarily Mediterranean group are the distinctive, clearly apomorphic male oblique frontal ridge and the more subtle character of a sclerotized patch on the inner face of the gonostylus, although each of these characters is weakly developed in some species.

A few smaller monophyletic units can readily be defined within this assemblage. One of the most distinctive of these has been referred to by Schwarz (1974, 1977) as the *fuscicornis* group, which consists of the species *fuscicornis, linsenmaieri, merceti, nitida, panurgina, panurginoides, polyacantha, rubricoxa, rufoabdominalis, sicula,* and *similis.* Schwarz (1977) has written a key to all the described species in this group. A distinctive morphological autapomorphy for the *fuscicornis* group is the apex of the female hind tibia (Character E in the preceding description, Figure 54; the setae are greatly reduced in size and not heavily melanized in *linsenmaieri*). The few species in this group whose hosts are known have the unusual, and presumably apomorphic, behavior of parasitizing panurgine bees. This *fuscicornis* group was included as a separate terminal taxon in the cladistic analyses, but it always was placed as the sister group of the *armata* group, which was paraphyletic with respect to it.

A small monophyletic assemblage of species most closely related to *armata* could be defined by a unique modification of the hind tibia, which is distinctly produced on the *inner* (posterior) face and bears conspicuously shortened tibial spurs of unequal length (Figure 66). Males of these species also have conspicuously enlarged front femora that are modified in a variety of ways (cf. *sanguinea* and *femoralis* in Figures 63 and 64).

Singling out these distinctive monophyletic units by naming them as separate groups would still leave the problem of how to deal with the remaining species that have the combination of male oblique frontal ridge, a flocculus on the hind femur, and a sclerotized patch on the inner face of the gonostylus. Until a detailed phylogenetic analysis of the entire group is undertaken, I prefer to name only the inclusive group whose monophyly was consistently supported in my cladistic analyses. The *armata* group is most diverse in the Mediterranean basin, with a few species extending into central and northern Europe.

As discussed in the cladistic analysis, the male subgenital brush, S8, and genitalia indicate that the *armata* group belongs within the complex of species groups at node B in Figure 8 or node C in Figure 14. The flocculus and vestiture of the gonostylus in several species suggest affinities with the *trispinosa* and *furva* groups, although it is most parsimonious to regard these isolated similarities as homoplastic.

Schwarz (1977) described two new species, *felici* and *lamellata,* that he considered to be closely related to *hirticeps,* described by Pérez in 1895. Schwarz (1981) also considers *N. plumosa* Gribodo to be closely related to these species. The only one of these three species for which the male is known is *felici.* It lacks oblique frontal ridges, a flocculus, and a sclerotized area on the inner face of the gonostylus, so I would not place it in the *armata-fuscicornis* lineage. However, the phylogenetic position of *felici* is far from clear. S8 is as in the *ruficornis* group, but the shape and vestiture of the gonostylus is not: there is no basoventral lobe or setal tuft, the vestiture is long but the setae are simple and relatively sparse, and there is a unique sharp, longitudinal ridge along the dorsal side of the gonostylus (Figure 171). Until the males of *hirticeps* and *lamellata* are described, I see little choice but to leave open the question of what the phylogenetic position of this putative lineage might be.

BIOLOGY: Host records are available for only a handful of species whose ranges extend into central Europe. The species *armata, femoralis,* and *mutabilis* are parasites of *Andrena,* although Stoeckhert (1932) considered the associations for the latter two species uncertain. Stoeckhert (1932), Bischoff (1927), and Perkins (1919) all reported *A. hattorfiana* as the host of *N. armata*; and Stoeckhert and Bischoff both regarded *A. humilis* as the host of *N. femoralis.* Both Bischoff and Stoeckhert listed *A. chrysopyga* as the host of *N. mutabilis.* In none of these records were the authors explicit about the supporting evidence. Presumably the associations that were considered well supported were based upon seeing the parasites in nest areas of their putative hosts in numerous localities and in more than one year. Friese (1923) proposed that *A. labiata* and *A. polita* were also hosts for *N. mutabilis,* but Stoeckhert (1932) considered this doubtful.

Three central European species in Schwarz's *fuscicornis* group,

fuscicornis, *panurgina* and *similis*, are parasites of *Panurgus*, with *N. fuscicornis* attacking *P. calcaratus*, *N. panurgina* on *P. dentipes*, and *N. similis* on *P. banksianus* (Stoeckhert, 1932). The host record for *N. fuscicornis* is one of the few European host associations corroborated by a nest excavation, although Stoeckhert only reported finding a fresh adult male inside a nest, and did not rear parasite adults from larvae found in the nest. Both *N. fuscicornis* and *N. similis* are active in middle to late summer in Germany, but species from southern Europe and North Africa have been collected as early in the year as February.

belfragei group

Nomada subgenus *Phelonomada* Snelling, 1986. Contrib. Sci., Los Angeles Co. Mus., 376: 24, 27-28. Type species: *Nomada belfragei* Cresson, 1878; original designation.

DESCRIPTION: As in *ruficornis* except for the following: (b) mandible rounded apically, without subapical tooth; (c) *first flagellomere equal to or longer than second*; (d) *preoccipital ridge evenly rounded, not angulate or carinate*; (i) lateral angle of pronotal collar rounded in female, angulate along crest of curve in male; (r) *procoxa with a short, conical or triangular process* (varies in prominence, occasionally absent); (s) incomplete lateral carina on procoxa; (t) *punctures on metasomal terga nearly contiguous, fine but distinct*; (u) *metasomal terga with narrow impunctate apical margin*. **Females**: (A) *paraocular ridge absent* (faintly discernible in *wheeleri* ssp. *engelmanniae* [holotype examined]). **Males**: (G) scape about as wide as flagellum; (U) inner basal shelf of gonostylus present, bearing short, stout, flattened setae.

COMMENTS: The species of this group were formerly assigned to the the subgenus *Micronomada* (= *vegana* group), because of shared similarities in several aspects of external morphology, such as the spinose procoxae and the absence of a paraocular ridge in females. However, Snelling (1986) called attention to structures of the pronotum and male terminalia that suggested a closer affinity to the genus *Nomada* as he defined it, and my cladistic analyses support Snelling's conclusions about the phylogenetic affinities of this small group.

BIOLOGY: No host records are available for the species in this group. Adults are active in late spring (April to June).

superba group

Holonomada Robertson, 1903. Canadian Entomol. 35: 174, 177. Type species: *Nomada superba* Cresson, 1863; original designation.

DESCRIPTION: As in *ruficornis* except for the following: (b) mandible simple, apex subacute (this state also occurs in most species of the *ruficornis* group, although not in *ruficornis* itself); (c) first antennal flagellomere longer than or equal to second; (g) *malar space always open posteriorly in male* (Figure 35), sometimes open posteriorly in female also (*the face is also very strongly protuberant below* in all species in this group, as shown in Figure 35); (s) incomplete lateral carina present on procoxa (occasionally absent or very short in *sexfasciata* and *fuscipennis*); (t,u) metasomal terga very closely and finely punctate, with very narrow impunctate apical margin; (y) vestiture of head and mesosoma relatively long and dense, erect, weakly plumose (as usual for *Nomada*, the vestiture is longer and denser in males than in females). **Females**: (A) paraocular ridge usually present, but absent or very weak in *lucidula*; (D) *pygidial plate parallel-sided, broadly rounded apically* (Figure 60, this state also occurs in the *basalis* group and sporadically in other *Nomada*, e.g. in the *vegana* group); (E) *apex of hind tibia with a dense cluster of numerous straight, slender, apically pointed, lightly melanized setae* (Figures 56, 57). **Males**: (G) scape cylindrical, as wide as or slightly wider than flagellum (this state also occurs commonly within the *ruficornis* group, although not in *ruficornis* itself); (I) protarsal brush often absent or weakly developed; (N) metasomal sterna usually with a distinct subapical fringe of erect, flexible, weakly plumose setae (absent or very weak in *cristata, fuscipennis, imperialis, lucidula, morawitzi*, and three undescribed North American species); (O) apex of pygidial plate rounded, not notched or emarginate; (P) S7 with apex subtruncate or weakly emarginate (Figures 169, 170); (U) inner basal shelf of gonostylus present, bearing a dense cluster of very short, stout, melanized setae (several species in the *belfragei, bifasciata*, and *ruficornis* groups also have similar setal clusters); (BB) usually no ridge on outer face of penis valves, but *fuscipennis* has an incomplete ridge very similar to that of the *odontophora* group.

COMMENTS: The North American species of this group correspond to Robertson's (1903) genus *Holonomada*, which subsequent North American workers (e.g. Evans, 1972; Hurd, 1979; Snelling, 1986) have generally treated as a subgenus of *Nomada*. The most recent species-level revision, published by Evans in 1972, recognized 14 species and subspecies. An additional five undescribed North American species and three undescribed Old World species that I have been able to examine would also be included in this group.

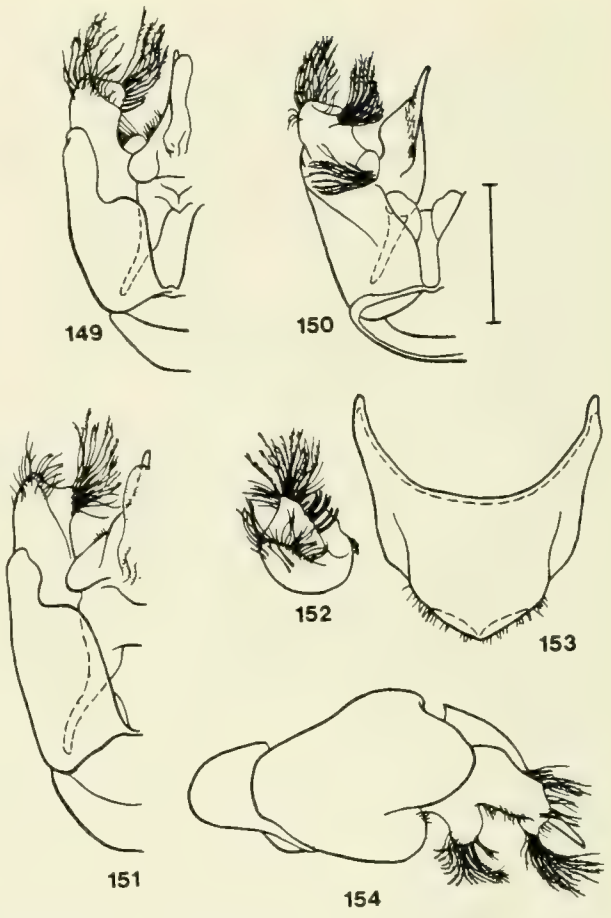
Snelling (1986, p.20) indicated that *Holonomada* also occurs in the Old World, but the affinities of the North American species placed in the subgenus *Holonomada* to Old World species groups, such as Schmiedeknecht's (1882) *sexfasciata* and *agrestis* groups, have not previously been noted or carefully examined. Snelling remarked that the North American species of this group form a "weak subgenus" that might need to be merged "with the nominate subgenus [= the *ruficornis* group] when the fauna of western North America becomes better known" (Snelling, 1986, p.20). An examination of the Palearctic species, especially those allied to *sexfasciata* and *basalis*, makes the distinction between these species and the *ruficornis* group even murkier.

One feature all the New and Old World species of the *superba* group share in common is large size and a robust body form, which is conspicuous but not a very reliable indicator of close phylogenetic relationship. It is also not restricted to species of the *superba* group. Rodeck (1945), followed by Evans (1972) and Snelling (1986), placed special emphasis on "*sides of propodeum with prominent projecting angles* just behind the propodeal spiracle, most readily seen in profile from diagonally above" (Rodeck, 1945, p. 179, author's italics). This character is indeed conspicuous in some North American species, such as *affabilis, henningeri, parkeri*, and *superba*, and it is certainly apomorphic, but it takes a leap of faith to perceive it in species like *grandis* or *edwardsii* (or, more precisely, to reliably distinguish between its putative presence in these species and its absence in all species outside the *superba* group). Similarly, several Old World species, such as *agrestis, imperialis, pictiscuta*, and *fumipennis*, have the character clearly expressed, but it is much weaker or absent in other Old World species. The cluster of setae at the apex of the hind tibia is consistently present and clearly apomorphic, but it also occurs in the *basalis* group, and in my cladistic analyses it was interpreted as a synapomorphy shared by these two groups. The same is true of the parallel-sided, apically rounded pygidial plate, which also exhibits homoplasy, since it occurs in distantly related taxa such as the *vincta* and *trispinosa* groups and some species of the *vegana* group. The relatively wide malar space and protuberant face are consistently present in the *superba* group and probably apomorphic, but they are also sporadically present in other species groups of *Nomada*, including *limassolica* and *nobilis* of the *basalis* group. Throughout the *superba* group, male S8 has a horizontal shelf with a dense fringe of long, narrow, anteriorly-directed setae at the base of the median process (Figure 81). However, this state is not strictly confined to the *superba* group, and there is a series of intergrading forms that are difficult to sep-

arate into discrete states. The truncate or weakly emarginate apical margin of S7 is fairly consistent within the *superba* group, but the polarity of this state is far from certain. In general, the male genital capsule of the *superba* group is indistinguishable from that of the *ruficornis* group. This readily distinguishes the *superba* group from the *basalis* group, but because the states in the *superba* group are plesiomorphic, they would indicate that the latter group is paraphyletic. Evidence for the monophyly of the *superba* group is not very strong. The best candidates for autapomorphies would be the open malar space and protuberant lower face, which exhibit homoplasy; the projecting angles on the sides of the propodeum, which are not clearly expressed in every species; and the form of S7, which is difficult to polarize and not strictly confined to the *superba* group. The included species constitute a relatively homogeneous assemblage within the *basalis-superba* lineage, but whether the *superba* group represents a monophyletic sister group of the *basalis* group, or a paraphyletic basal assemblage, cannot be established without a more detailed analysis of the entire lineage.

BIOLOGY: The only definite North American host record (based on rearing the parasite from the nest of the host) is for *N. edwardsii*, which parasitizes *Andrena perimelas* (Linsley & MacSwain, 1955). Evans (1972) collected a female of *N. edwardsii* as it was entering a burrow of *Andrena placida*, but he did not rear parasites from the nest.

Snelling (1986, p.20) suggested that *N. hemphilli* may parasitize the eucerine anthophorid *Synhalonia amsinckiae*. He based this suggestion on the observation that over a ten year period the two species were active at the same time and in the same area, and "no *Andrena* of suitably large size was encountered at the appropriate time of year". Snelling's suggestion is particularly interesting in view of the fact that the only European species of the *superba* group for which a host association has been clearly established, *N. sexfasciata*, is a parasite of *Eucera longicornis* and perhaps *E. tuberculata* (Smith, 1876; Perkins, 1919; Stoeckhert, 1932). Smith (1876) found two specimens (it is not clear from his paper if these were pharate or eclosed adults) of *N. sexfasciata* in cells of *E. longicornis* that were excavated in April, just before the normal flight period of these species. Friese (1923) also reported species of *Eucera* as hosts of *N. agrestis* and *N. imperialis*, but he did not indicate the evidence upon which the association was based. Since he frequently based host associations on dubious criteria such as collecting both species on the same flowers at the same time of year, these associations still need to be conclusively demonstrated.



Figs. 149-154: Male genitalia and associated sterna in the *basalis* group. **Fig. 149.** Genital capsule, dorsal view, *N. basalis*; **Fig. 150.** Same, ventral view; **Fig. 151**. Genital capsule, dorsal view, *N. nobilis*; **Fig. 152.** Left gonostylus, seen looking down longitudinal axis of genital capsule, *N. nobilis*; **Fig. 153.** S7, ventral view, *N. basalis*; **Fig. 154**. Genital capsule, lateral view, *N. nobilis*. Scale bar = 0.5 mm.

basalis group

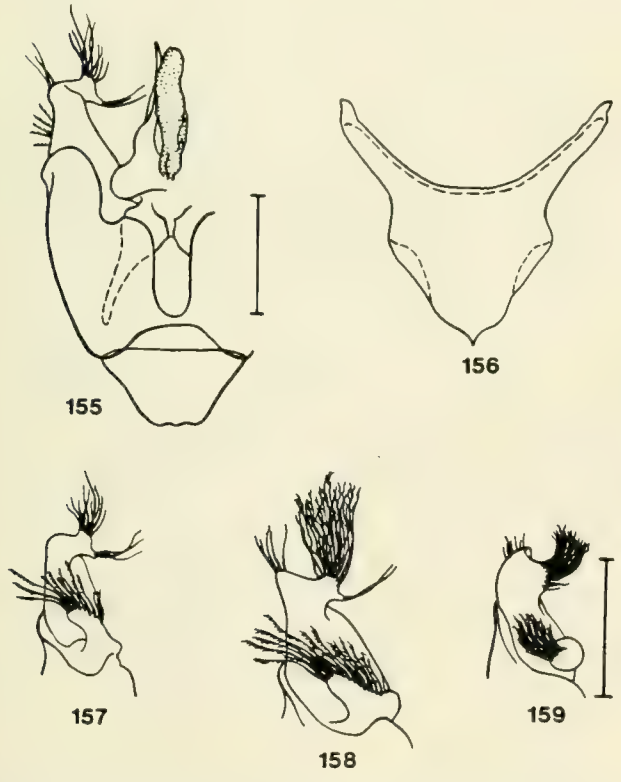
?*Nomada* subgenus *Laminomada* Rodeck, 1947. Ann. Entomol. Soc. America 40: 266. Type species: *Nomada hesperia* Cockerell, 1903b; original designation (see Comments section).

DESCRIPTION: As in *ruficornis* except for the following: (b) mandible simple, apex broadly or narrowly rounded; (c) first flagellomere usually distinctly longer than second, occasionally the two segments are of equal length; (g) malar space closed posteriorly in both sexes, face not strongly protuberant below, except in *limassolica* and *nobilis* (this distinguishes most species of the *basalis* subgroup from the closely related *superba* subgroup); (o) scutellum usually right-angled in profile, but distinctly flattened in *nobilis* (although there is still a weak posterior face), evenly convex in *desertorum* and an undescribed species; (p) sculpturing of propodeal enclosure variable: often as in other *ruficornis* group species, but mostly shagreened with basal rugulae very fine or absent in *insignipes*, *nobilis*, and some individuals of *basalis*, *mocsaryi*, and two undescribed species; (r) weak procoxal spine present in *desertorum* and *insignipes* (and *hesperia*, see Comments below); (t,u) sculpturing of metasomal terga usually as in *superba* group, but state in *cherkesiana* and *lateritia* is more like *ruficornis*; (y) vestiture of males consistently as in species of the *superba* subgroup, but greatly reduced in females of a few species (e.g. *basalis*, *lateritia*, *mocsaryi*). **Females**: (A) paraocular ridge usually present, but absent in *nobilis*; (D) pygidial plate parallel-sided, apex broadly rounded (as in *superba* group); (E) *apical setae of hind tibia as in* superba *group* (in *insignipes* and *mocsaryi*, the setae are further modified in ways that can readily be interpreted as derivatives of a *superba*-like groundplan state). **Males**: (G) antennal scape cylindrical, as wide as or slightly wider than flagellum; (I) protarsal brush absent or weakly developed (as in *superba* group); (J) front femur unmodified except in *hesperia* (Figure 62, see Comments below); (N) dense subapical setal fringe usually present on metasomal sterna (as in *superba* group), but weak or incomplete in *cherkesiana* and *insignipes*, absent in *desertorum*; (O) apex of pygidial plate rounded, not notched or emarginate (as in *superba* group); (P) S7 variously modified, *with various acute or narrowly rounded apicomedian processes* (Figures 153, 156), not truncate or emarginate as in *superba* subgroup; (T) gonostylus variously modified (Figures 149 - 152, 154, 157 - 159), never cylindrical throughout, *usually flattened at least apically and with a distinct ridge or keel on the inner face basally*; (V) vestiture of gonostylus variable, always with at least some long, api-

cally plumose or sinuate setae, *sometimes with a few very stout, flattened, long, bladelike setae along the inner face of the gonostylus* (e.g. *japonica, nobilis*, Figure 151, 152), *setae sometimes separated into basal and apical tufts* (e.g. *cherkesiana, limassolica, keroanensis*, and *sybarita*, as in Figures 157 - 159); (FF,GG) invagination and inner dorsal lobe of gonocoxite present but often weak, *median sinus parallel-sided and relatively narrow* (Figures 149, 155).

COMMENTS: Many species in this group are generally similar in overall appearance to those of the *superba* group, and the two taxa were consistently grouped together in the cladistic analyses. As discussed above, synapomorphies uniting the two groups are the apical setae of the female hind tibiae, the broadly rounded female pygidial plate, and the subapical setal fringe on the male metasomal sterna. Although not used as a character in the cladistic analyses, the species of the *superba* and *basalis* subgroups share a similar long, relatively dense vestiture of the head and mesosoma (the vestiture is secondarily reduced in females, but not males, of a few species in the *basalis* group).

The *basalis* group is considerably more heterogeneous in general appearance than the *superba* group, and is distinguished from its sister taxon primarily by characters of the male genitalia and associated sterna, especially the form of S7 and the shape and vestiture of the gonostylus. As in the *integra* group, male genitalia in the *basalis* subgroup vary considerably among species and might prove to be useful species-level characters, although there has not yet been a comprehensive revision of this group comparable to Schwarz's (1967) revision of the *integra* group. Because the species here placed in the *basalis* group do not share a uniform apomorphic state of these male genitalic characters, it is debatable whether the various modifications represent a single transformation series reflecting a sequence of changes within one lineage, or are independently derived, in which case the *basalis* subgroup would be an artificial, polyphyletic assemblage. In some cases, such as the similarities in the genitalia of *incisa, limassolica*, and *keroanensis*, the similarities in elaborate, complex shapes of the gonostylus and S7 are close enough that they seem very likely to be homologous, but it is far less clear whether these shapes are derived from, or ancestral to, those of such species as *basalis* and *nobilis*.



Figs. 155-159: Additional examples of male genitalia in the *basalis* group. **Fig. 155.** Genital capsule, dorsal view, *Nomada limassolica*; **Fig. 156.** S7, ventral view, *N. limassolica*; **Fig. 157.** Right gonostylus, ventral view, *N. limassolica*; **Fig. 158.** Same, *N. incisa* (same scale as Fig. 159); **Fig. 159.** Same, *N. keroanensis*. Scale bar = 0.5 mm.

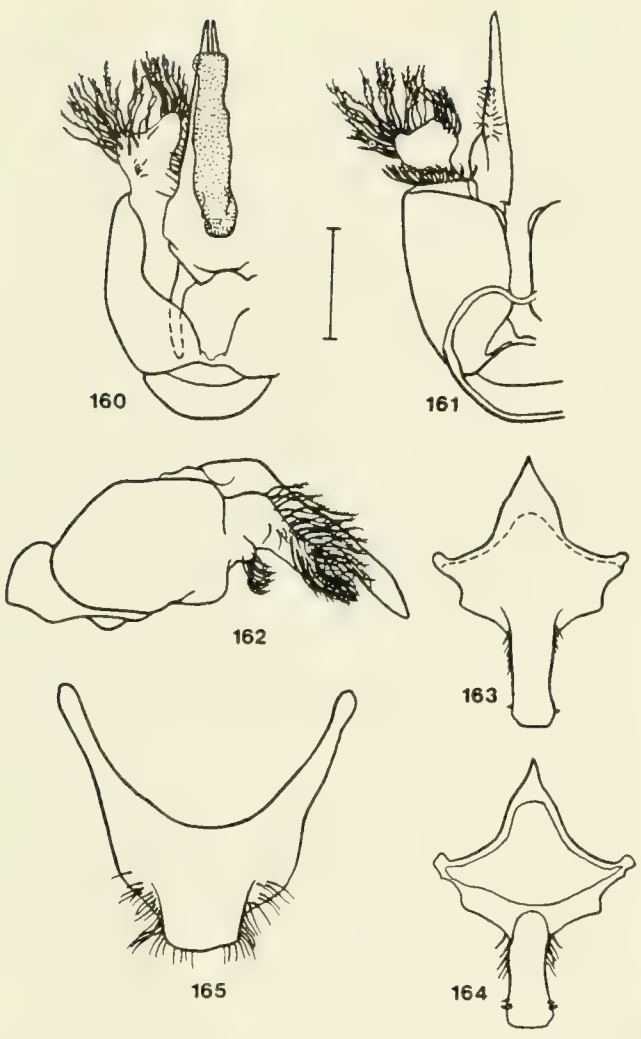
Two of the most problematic species are *hesperia* and *flavinervis*. The former species occurs along the Pacific coast of North America, and was placed in its own monotypic subgenus, *Laminomada*, by Rodeck in 1947. Snelling (1986), working within the frame of reference of New World species of *Nomada*, considered it most closely related to the subgenus *Holonomada* (= the *superba* group). The male of *hesperia* has striking apomorphic modifications of the front and middle femora that are completely unlike any other New World *Nomada*, although several Old World species in the *furva* and *armata* groups have equally striking modifications of the front femora. The gonostylus of *hesperia* is rather like that of some *basalis*-group species, such as *sybarita*; but this state also occurs in the less-modified species of the *bifasciata* group, such as *goodeniana* or *succincta*, and in the *trispinosa* group. The fact that *hesperia* is the *only* New World species with character states that might place it in the *basalis* group also raises doubts about whether the modifications of its gonostylus are homologous with those of the Old World species.

The Mediterranean species *flavinervis* does not pose the same biogeographic problems as *hesperia*, but its phylogenetic position is equally problematic. The genitalia of *flavinervis* are very unusual (Figures 160 - 165). The penis valves and S8 are unlike those of any other *Nomada* I have seen, but the gonostylus and dorsal gonocoxite could be interpreted as falling within the range of variation found in the *basalis* group.

Most of the species in the *basalis* group occur in the Mediterranean basin and arid regions of southwestern Asia. One species, *japonica*, is common in Japan and eastern Asia.

BIOLOGY: Bischoff (1927) and Stoeckhert (1932) both listed *Andrena nasuta* as a host of *Nomada nobilis*, although neither of them provided any evidence to support the putative relationship, and Bischoff indicated that he considered the association doubtful. Stoeckhert noted that *N. nobilis* must also utilize other hosts, since *A. nasuta* does not occur in some parts of southern Europe where *N. nobilis* has been collected.

Nomada japonica is reported to be a parasite of the eucerine bees *Eucera sociabilis, Tetralonia nipponensis* (Masuda, 1940; Hirashima, 1972) and probably *Eucera spurcatipes* (Maeta et al., 1987). A curious feature of *N. japonica* is that although it is quite common in Japan, males have never been collected there (Tsuneki, 1973). However, males of *N. japonica* have been recorded from the Ryukyu islands south of Japan (Tsuneki, 1973) and from Korea (Hirashima, 1960), and a large series of specimens from China in the USNM collection (determined by M. Schwarz) has about equal numbers of both sexes. Hirashima (1972) suggested that *N. japonica* might be thelytokous in Japan, and Maeta et al. (1987) have recently supported this hypothesis with data from dissections of 119 females from Japan. Although almost all of them had full grown and chorionated oocytes in the ovarioles, none of them had spermatozoa in the spermathecae. Furthermore, the spermatheca of *N. japonica* in Japan is significantly smaller, relative to body size, than that of 11 other Japanese species of *Nomada* examined by Maeta et al.



Figs. 160-165: Male genitalia and associated sterna of *Nomada flavinervis*. **Fig. 160.** Genital capsule, dorsal view; **Fig. 161.** Same, ventral view; **Fig. 162**. Same, lateral view; **Fig. 163**. S8, ventral view; **Fig. 164.** S8, dorsal view; **Fig. 165.** S7, ventral view. Scale bar = 0.5 mm.

(they did not examine *N. japonica* from mainland populations with males).

bifasciata group

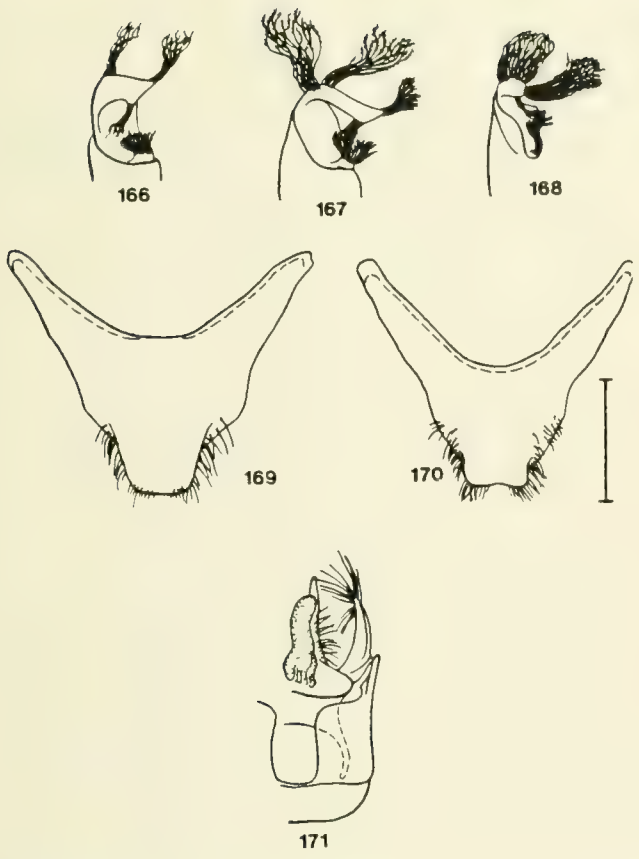
DESCRIPTION: As in *ruficornis* except for the following: (b) mandible simple, apex subacute to broadly rounded; (c) relative length of first two flagellomeres variable, but most often the two are equal in length in females, whereas the first is shorter than the second in males; (d) preoccipital ridge carinate, although relatively broad rather than a sharp, narrow carina; ridge remains prominent lateroventrally, so that in profile the back of the head is distinctly angulate below; (g) malar space closed posteriorly (or narrowly open in some males); (m) metapleuron not protuberant above (or sometimes weakly protuberant in *nigroflavida* and *succincta*); (r) procoxal spine absent (weak triangular process present in some individuals); **Females**: (E) *apex of hind tibia distinctly produced, with two or three short, flat, curved, apically rounded, closely spaced or overlapping setae* (as in Figure 58). **Males**: (G) scape cylindrical, usually about same width as flagellum, but slightly wider in *goodeniana, numida*, and *succincta*; (K) *base of hind femur with a small concavity bearing a dense mat of short, appressed setae which are broadened and flattened basally; and hind trochanter with a prominent flocculus of long, flexible, plumose setae* (Figure 68); (L) *subgenital brush restricted to apical margin of S6, setae laterally directed rather than erect* (Figure 7h); (M) *apical margin of S6 with a distinctly narrowed median process* (Figure 7h); (O) apex of pygidial plate emarginate or distinctly notched; (T) gonostylus variable in shape, with a continuous sequence of forms ranging from cylindrical and apically rounded as in *ruficornis* group (e.g. *succincta*) to *flattened, strongly curving in toward midline of genital capsule, and obliquely truncate at apex* (e.g. *bifasciata*; see Figures 166 - 168); (U) inner basal shelf on gonostylus present, with or without a dense cluster of very short, stout, melanized setae; (V) vestiture of gonostylus always long, dense, and apically sinuate or plumose, with a continuous series of states ranging from a more or less uniformly dense covering like in the *ruficornis* group (e.g. *succincta*), through a distinct separation into basal and apical tufts (e.g. *nigroflavida*, Figure 168) to a further separation of the apical tuft into two tufts (e.g. *bifasciata*, Figure 166); (W,X) ventral base of gonostylus with a distinct cylindrical lobe bearing a dense tuft of long, apically plumose seta (may be subdivided into two tufts).

COMMENTS: Bees in this group are large to medium-sized, with very coarse, dense punctation on the head and thorax, so that in general appearance they are similar to many of the robust species in the *ruficornis, superba*, and *basalis* groups. In the form of the subgenital brush and genitalic characters, especially the shape and vestiture of the gonostylus, the *bifasciata* group exhibits states that can readily be interpreted as intermediate between the *ruficornis* and *furva-trispinosa* groups. There are also states of the gonostylus in some species, such as *bifasciata*, that are clearly autapomorphic.

Despite the continuous range of variation in genitalic characters, two character states are consistent within the *bifasciata* group and clearly apomorphic, thus providing evidence that this is a monophyletic group. These character states are the distinctive apical setae on the female hind tibia and the unique setal modifications on the male hind trochanter and femur (Figure 68). A few North American species, such as *imbricata* and *luteoloides*, have the overall appearance of species in the *bifasciata* group, and the female hind tibiae have the same distinctive apical setae (Figure 58). However, the males lack any of the apomorphic modifications of the hind legs, subgenital brush, or gonostyli. Given the observed variation in the genitalic characters among Old World members of this group, one might argue that these North American species could be regarded as the most plesiomorphic members of the *bifasciata* group. I prefer not to include them, since to do so would leave only one diagnostic apomorphic trait, the female apical hindtibial setae, to define the group. (Other similarities, such as the carinate preoccipital ridge and coarse sculpture, are characters that are either plesiomorphic or very likely to exhibit homoplasy throughout the genus.) Because the type of male flocculus in the Old World species is so consistent, distinctive, and clearly apomorphic, I consider it a necessary diagnostic character for defining the *bifasciata* group, at least until a cladistic analysis that includes the problematic North American species can be done.

As defined here, the *bifasciata* group is restricted to the Palearctic, with its greatest diversity in the Mediterranean region. *Nomada goodeniana* is very widely distributed across Eurasia, extending from the British Isles to Siberia. The Japanese species *comparata* clearly belongs in the *bifasciata* group as well.

BIOLOGY: Host associations have been reported for the common European species *bifasciata, fucata, goodeniana*, and *succincta* (Perkins, 1919; Bischoff, 1927; Stoeckhert, 1932; records summarized in



Figs. 166-168:. Ventral views of right gonostylus in the *bifasciata* group, freehand drawings: **Fig. 166**. *Nomada bifasciata*, **Fig. 167.** *N. accentifera*; **Fig. 168.** *N. nigroflavida*; **Fig. 169.** Male S7, ventral view, *N. sexfasciata* (*superba* group); **Fig. 170.** Male S7, ventral view, *N. edwardsii* (*superba* group). Scale bar = 0.5 mm.for Figs. 169, 170; **Fig. 171.** Genital capsule, dorsal view, *N. felici*. Freehand drawing.

Alexander, 1991). All are considered to be parasites of *Andrena*, primarily on the basis of repeated observations of the parasites in association with their putative hosts.

The host of *N. fucata* in central Europe and Great Britain is *Andrena flavipes*, which is bivoltine over much of its range (Perkins, 1919; Stoeckhert, 1932). According to Perkins, *N. fucata* in England is much more local in distribution than its host, and it only parasitizes the second generation of *A. flavipes*. In Germany the parasite is more common and routinely parasitizes both generations of its host, although Stoeckhert (1932) reported that it was much less abundant in the first generation. This is in contrast to the pattern in most bivoltine *Nomada*, which are usually more abundant in the first generation. The two generations of *N. fucata* are also morphologically distinctive, with the spring generation exhibiting much longer vestiture on the head and thorax (M. Schwarz, personal communication).

trispinosa group

DESCRIPTION: As in *ruficornis* except for the following: (b) mandible simple, apex broadly to narrowly rounded; (c) relative length of first two flagellomeres variable even within species; usually the two are about equal in length or the first is slightly longer than the second; (d) preoccipital ridge usually angulate, but rounded or weakly angulate in *trispinosa* and three undescribed species; (f) base of proboscideal fossa somewhat narrowed, but basically rounded, not slitlike; (h) median portion of pronotal collar angulate (*hera, nipponica*) or *greatly constricted and pressed up against scutum* (as in *furva* group); (i) lateral angle of pronotal collar rounded when viewed from in front, but angulate along crest of curve, and somewhat recessed or "pinched back" (as in *furva* group); (o) scutellum variable, with distinct horizontal and posterior faces in *trispinosa, nipponica*, and three undescribed species, but evenly convex in profile in the other species; (p) propodeal enclosure with distinct rugae basally, usually shagreened or finely rugulose apically (apically polished, resembling *integra* group, in *nipponica*); (s) short, incomplete lateral carina present on procoxa. **Females**: (E) *distal setae of hind tibia very short, stout, broadly rounded apically, number varying from two or three in most species (Figure 55) to twenty or more in* nipponica. **Males**: (F) *flange at anterior articulation of mandible very strongly developed* (resembling state of some North American species of the *vegana* group, but never flattened and disclike as in many neotropical species of that group); (G) scape cylindrical, not conspicuously enlarged; (I) protarsal brush variable, absent or very weak in most species, setae sparse but long in those species where it is best developed, like *trispinosa, hera*, and *brevis*; (K) *base of hind femur concave on ventral face, without a distinct flocculus, but with a few recumbent setae within the concavity and with anterior and posterior ventral rows of long, flexible, plumose setae, vaguely suggestive of an incomplete scopa* (Figure 65) (in *nipponica* and an undescribed species, the setae of the anterior row are sparse and recumbent, so the state is similar to a weakly developed flocculus as in many species of the *furva* group); (L) subgenital brush variable: most often with dense apical fringe of setae (as in *bifasciata* group), but median tuft is virtually absent in one undescribed species (so that the subgenital brush resembles that of the *furva* group), and brush in *nipponica* has lateral fringe weak and median tuft well developed, extending onto the disc of S6 (thus, it is indistinguishable from the subgenital brush of the large *ruficornis* complex); (O) pygidial plate variable, but usually weakly emarginate apically; (P) S7 not specially modified in a consistent manner throughout the group (apical margin distinctly recurved in five species); (Q,R,S) median process of S8 laterally compressed, parallel-sided at base, *apex distinctly expanded, often hiding spinose setae in ventral view* (Figure 83); lateral profile of S8 not angulate; (T) gonostylus cylindrical, long but of variable width, *very distinctly curved toward midline of genital capsule* (as in *furva* group); (U) inner basal shelf usually present on gonostylus (absent in *polemediana*, weak in several species); (V) *vestiture of gonostylus consists of long, apically plumose or sinuate setae separated into distinct basal and apical tufts* (as in *furva* group) (basal tuft is absent or extremely sparse in *brevis*); (W) basoventral lobe on gonostylus always present, *usually a transverse ridge or at least somewhat flattened in cross section* (long and cylindrical in *nipponica*); (EE) apex of penis valves acute, *entire valve in lateral view conspicuously lenghtened* (Figure 84).

COMMENTS: This small group seems to have a primarily Mediterranean distribution, although the Japanese species *nipponica* is included in the group on the basis of male genitalic characters (especially the gonostyli and penis valves) and the form (but not the number) of the distal setae on the female hind tibiae. I have not been able to examine the species *babai* or *xanthopoda* recently described by Tsuneki and Schwarz, respectively. They are tentatively placed here because the description of each species explicitly states that it is closely related to species in this group. The BMNH has a series of specimens from China (collection localities range from the Szechwan Basin to Beijing) that Schwarz has labelled as an unnamed subspecies of *trispinosa*.

The male genitalia indicate an affinity with the *furva* group, and in the cladistic analyses the *trispinosa* and *furva* groups always clustered together. The monophyly of the *trispinosa* group is supported by the distinctive distal setae of the female hind tibia

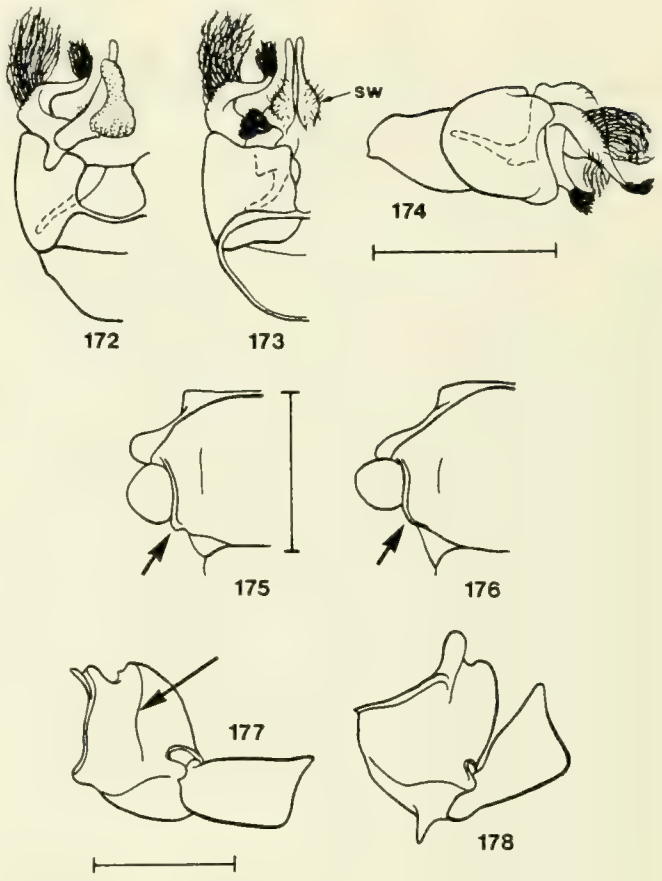
(although the setae are similar in *fuscicornis* and its close relatives within the *armata* group), the vestiture of the male hind femur, the form of the penis valves, and perhaps the modification of the apex of the median process of S8 in males. In addition to the eight named species listed in the catalog of Alexander and Schwarz (1994), Schwarz has identified at least five species that are still undescribed.

BIOLOGY: Westrich (1989) cites two published records of *Andrena taraxaci* as the host of *N. trispinosa* (Friese, 1888; Kocourek, 1966). Friese based the association on collecting both species on the same flowers (*Leontodon*), whereas Kocourek reported two large aggregations of *A. taraxaci* nests in which *N. trispinosa* was abundant and freely entered the nests without meeting any resistance from the *Andrena*. Friese (1923) also reported *N. trispinosa* as a parasite of *Andrena truncatilabris*, on the basis of finding both of them visiting flowers of *Sisymbrium columnae* and *Salvia* in May and June near Budapest. Neither Westrich nor Kocourek repeated this dubious association. In view of its apparent phylogenetic closeness to the *furva* group, it would be especially interesting to know if species of the *trispinosa* group ever parasitize halictids. Species in this group are active in spring and early summer (late February to early June).

furva group

Includes *furva* group of Stöckhert, 1943. Deutsche Entomol. Zeitschr. 1943: 89-126.

DESCRIPTION: As in *ruficornis* except for the following: (a) labrum usually wider than long, but definitely longer than wide in *bouceki*, *erythrocephala*, and *yarrowi*, about as long as wide in *cordilabris* (according to Figure 69 in Schwarz, 1990); (b) mandible simple, apex subacute or rounded; (c) relative length of first two flagellomeres variable: usually the two are about equal in length or the first is longer than the second, but in some species from the Philippines, Indonesia, and New Guinea the first segment is distinctly shorter than the second; (d) *preoccipital ridge angulate or sharply carinate*; (f) base of proboscideal fossa usually constricted by mesally-directed hypostomal carina (broadly rounded in *yarrowi* and an undescribed species, only weakly constricted in species allied to *glaucopis*); (h) median portion of pronotal collar usually greatly constricted and pressed against scutum, but somewhat broader and carinate in *blepharipes*, *collarae*, and an undescribed species (collar also greatly constricted medially in *trispinosa* group and a few species of *roberjeotiana* group); (i) lateral angle of pronotal collar rounded when viewed from in front, but angulate along the crest of the curve, weakly recessed as if pinched back toward the scutum (this state also occurs in the *trispinosa* group); (k) anterior margin of pronotum varies from evenly rounded to angulate even within species; (o) scutellum variable, ranging from right-angled to evenly convex in profile; (p) sculpturing of propodeal enclosure variable, although always distinctly rugose or reticulate basally (very few rugae in *priesneri*); apical portion of enclosure highly polished in several species, entire enclosure reticulate or rugose in several species; (q) distinct ridge usually present on lateral margin of propodeal enclosure (Figure 42), although it is often weak or absent basally, and completely absent in *kocoureki*, *malayana*, *blepharipes*, *cypricola*, and *guichardi*; (s) no outer lateral carina on procoxa, but inner dorsal carina usually present on Oriental and Australian species (Figure 177, arrow); (t) *metasomal terga usually polished and impunctate or very weakly punctate* (punctures very weak but dense in *cypricola* and *erythrocephala*, moderately dense in *blepharipes*, *discedens*, *guichardi*, *sutepensis*, and males of *bouceki*); (u) metasomal terga with broad impunctate apical margin; (v) vein 1st r-m of forewing usually present, but absent in *attrita*, *dissessa*, *makilingensis*, *palavanica*, and *pervasor* (all from the Philippines) and *bicellula* from Sri Lanka; (y) *vestiture of mesosoma usually includes dense patches of long, thickly plumose, recumbent white setae on the mesepisternum and/or the lateral angles of the propodeum* (Figure 42; similar vestiture also occurs within the *ruficornis* group). **Females**: (E) apical setae of hind tibia long, straight (in many species there is one very long, narrow, almost bristlelike seta in addition to a few shorter, stouter setae). **Males**: (F) anterior articulation of mandible with a distinct flange; (G) scape cylindrical, about as wide as flagellum or slightly wider; (I) protarsal brush usually present, although very weak or absent in *banahaonis* and *sutepensis*; (J) front femur usually not modified, but greatly enlarged and concave anteriorly in *cypricola*, *erythrocephala*, and *laticrus*; (K) base of hind femur usually with a flocculus, although it varies considerably in prominence and may be only a very weak tuft (extremely weak or absent in most species in the Oriental and Australian region); (L) *subgenital brush with very dense, prominent, lateral tufts of long, flexible, horizontally-directed setae; median tuft inconspicuous, setae extremely short and fine* (Figure 7g);



Figs. 172-178: *Nomada furva* group: **Fig. 172.** Genital capsule, dorsal view, *Nomada distinguenda*; **Fig. 173.** Same, ventral view; **Fig 174.** Same, lateral view; **Fig. 175.** Dorsal view of mesosoma, *N. australensis* (*furva* group). Arrow shows supra-alar carina, which projects posterad in Indoaustralian species of the *furva* group; **Fig. 176.** Dorsal view of mesosoma, *N. panurgina* (*armata* group). Arrow shows supra-alar carina, which does not project posterad; **Fig. 177.** Posterior view of right procoxa of *N. adusta* (*furva* group). Arrow shows the inner dorsal carina that characterizes Indoaustralian species of the *furva* group; **Fig. 178.** Posterior view of right procoxa of *N. articulata* (*erigeronis* group), illustrating the common condition in *Nomada*, with no inner dorsal carina; **sw** = basoventral swelling on penis valve; Scale bar = 0.25 mm. for Figs. 172 - 174 ; 0.5 mm for Figs. 177, 178; 1.0 mm for Figs. 175-176

(O) pygidial plate notched or emarginate apically (emargination very weak in *cypricola* and *connectens*); (P) S7 variable, no apomorphic state consistently present throughout group; (Q,R,S) *median process of S8 laterally compressed, narrow, parallel-sided, greatly shortened* (Figure 79), with spinose setae, not angulate in lateral view; (T) *gonostylus long, narrow, cylindrical, distinctly curved toward midline of genital capsule* (Figures 172, 173: this same state occurs in the *trispinosa* group); (U) shelf present on inner base of gonostylus, but without a cluster of specialized setae; (V) *vestiture of gonostylus consists of long, dense, apically plumose setae separated into distinct basal and apical tufts* (Figures 172, 173: this same state occurs in the *trispinosa* group); (W) *ventral base of gonostylus with a distinctly transverse lobe* (Figure 173); (DD) *basoventral swelling present on penis valves* (Figure 173, **sw**).

COMMENTS: This is a large group whose monophyly is supported by unique apomorphic states of the male genitalia (the basoventral swelling on the penis valves) and S8 (the greatly shortened median process), although variability in the first of these characters limits its usefulness as a consistent diagnostic character. The male subgenital brush is very distinctive and uniform throughout the *furva* group, although some species in the *trispinosa* group have a very similar subgenital brush. The shape and vestiture of the gonostylus are synapomorphies shared by these two groups. Certain externally visible characters are useful in diagnosis, although they exhibit homoplasy and thus need to be used in conjunction with the genitalic characters for certain identification. These characters include the carinate preoccipital ridge, the constricted base of the proboscideal fossa, the mesosomal vestiture, and the punctation of the metasomal terga. The sculpturing of the propodeal enclosure is too variable to be really reliable, but the majority of species have a distinct ridge marking the lateral margin of the propodeal enclosure. Finally, the majority of species are among the smallest in the genus, on the order of 5 - 7 mm. in body length, and even the largest species, such as *erythrocephala* and *blepharipes*, rarely exceed 10 mm.

The *furva* group is restricted to the Old World, but it occurs throughout the Palearctic and is the only group present in Southeast Asia, the Malay Archipelago, New Guinea, and Australia. The Indoaustralian species almost certainly constitute a monophyletic lineage, although the apomorphic characters supporting this are fairly subtle or difficult to see: an inner, dorsal carina on the procoxa (Figure 177); the supra-alar carina produced posterad rather than curving mesad to merge with the scuto-scutellar suture anterad of the axilla (cf. Figures 175 and 176); and a broad, shallow sulcus extending anteroventrally from the scrobe to the pre-episternal sulcus (this is often obscured by dense vestiture on the mesepisternum).

The species list in Alexander and Schwarz's (1994) catalog would indicate that the Oriental region is the center of diversity for the *furva* group, but it is difficult at present to know how many species really exist in that region, because the taxonomic status of the populations of the many islands of the Malay Archipelago and the southwestern Pacific remains problematic. Schwarz (1990) published a revision of species from part of the Oriental region, but he did not deal with species that have been described from Malaysia, Indonesia, Taiwan, the Philippines, New Guinea, or the Solomon Islands. Two species described from India, *lucilla* Nurse and *lusca* F. Smith, are also not discussed in Schwarz's paper. The number of specimens available to study is limited, but a large number of species have been named, especially by Cockerell. The list in Alexander and Schwarz's catalog includes all the names I have found for *Nomada* from this region, and I have examined the types of most of them, including all but one of those described by Cockerell. Thus I can say that these taxa definitely belong in the *furva* group, although I cannot say how many of them should be considered valid species. Names preceded by a question mark in that list represent taxa for which I have not seen types or accurately determined specimens. They are provisionally included primarily on the basis of their geographic distribution, as well as the limited amount of relevant information contained in the original descriptions.

The *furva* group also has many species in the Mediterranean region. Besides those listed in Alexander and Schwarz (1994), I have examined an additional twenty undescribed species in the personal collection of M. Schwarz. A few species in the group range northward as far as Germany and the British Isles, and Stöckhert (1943) has revised the species of central Europe, where he recognized 7 species. The minute species *sheppardana* extends from Britain to Japan, with several locally differentiated populations described as subspecies. Two other Japanese species, *pulawskii* and *taicho*, also belong in the *furva* group.

BIOLOGY: The only reasonably well documented host associations are for the more common species of central Europe (Stoeckhert, 1932) and Great Britain (Perkins, 1919). The species *furva, sheppardana* (= *dalii*), and *distinguenda* have frequently been mistaken for one another (Stoeckhert, 1932), which adds to the difficulty of interpreting reported host associations. According to Stoeckhert, the proper host associations are as follows: *N. furva* parasitizes *Lasioglossum (Evylaeus) morio* and *L. (E.) leucopum* ; *N. furva nigricans* parasitizes *L.(E.) punctatissimum*; *N. sheppardana* (referred to as *dalii* by Stoeckhert) parasitizes *L.(E.) nitidiusculum*; *N. distinguenda* parasitizes *L.(E.) villosulum*, and *N. kohli* parasitizes *L.(E.) puncticollis*. Perkins (1919) also reported *L.(E.) nitidiusculum* in Britain as the host of *N. sheppardana* (which he called *furva*). [There is no consensus on generic boundaries within the Halictinae. Stoeckhert assigned all the host species to the genus *Halictus*, but the classification of Ebmer (1976) is used here.]

Stoeckhert (1932) reported that *N. furva, N. distinguenda*, and *N. kohli* are bivoltine, and he suggested that *N. sheppardana* probably is as well. In *N. furva* and *N. kohli*, he found the spring generation to be much more abundant than the summer generation, whereas in *distinguenda* both generations are about equally abundant. According to Knerer (1968), the hosts of *N. furva* and *N. kohli* are eusocial. Knerer also considered *L.(E.) villosulum*, the host of *N. distinguenda*, to be eusocial. However, subsequent detailed studies by Plateaux-Quenu and Plateaux (1986) have established that *L.(E.) villosulum* is not eusocial, despite the fact that it exhibits some traits usually associated with eusocial species. (For example, females of the summer generation are much smaller than the spring females, and the sex ratio of the summer generation is heavily female-biassed.)

These observations raise the intriguing question of whether the observed differences in the abundance of the second generation of different *Nomada* species are related to differences in the social behavior of their hosts, since the parasites whose numbers are said to be much lower in the second generation are the species that attack eusocial hosts. It would be especially interesting to know how many species in the *furva* group parasitize eusocial hosts, and whether they have developed ways of entering guarded nests, or depend primarily on attacking nests at the start of the seasonal cycle while they are still solitary.

DISCUSSION

In *The Origin of Species*, Darwin (1859, Chapter 13) argued that "the characters which naturalists consider as showing

true affinity between any two or more species, are those which have been inherited from a common parent, and... all true classification is genealogical". Most systematists in the past century and a half have found this argument persuasive and have attempted to base classifications upon inferred phylogenetic relationships. The hypothesis that a given group of organisms is descended from a unique common ancestor is based upon observed similarities shared by those organisms. If a large number of similarities are found, or if similarities that are in some way qualitatively "special" are identified, this increases our confidence that the most plausible explanation for why these similarities are found only in these organisms and in no others is because they have been inherited from a unique common ancestor. Parsimony algorithms are a mathematical formulation of this line of reasoning. The basic objective of a parsimony analysis is to explain the distribution of as many independent shared similarities as possible by hypotheses of homology, and to minimize the number of shared similarities that must be explained by other causes, such as convergent adaptations to a similar selection pressure (Farris, 1983).

The stipulation that the characters should be independent of one another is an important element in the persuasiveness of the argument. The power of natural selection to produce similar solutions to similar selection pressures is considerable, but it is not expected to be absolute. For example, selection leading to modifications of the mouthparts for obtaining nectar from a certain type of flower would not be expected to simultaneously change the antennae, genitalia, integumental sculpturing, and wing venation. This is why systematists advocate basing phylogenetic hypotheses upon as many different characters as possible. Admittedly, organisms are not tinker toys composed of pieces that can be rearranged at will. Changes in any given structure should always be constrained to some degree by the need for the entire organism to function as an integrated whole. Furthermore, as Gould (1977) has argued at length, adult morphologies are the endpoints of complex developmental sequences, and selection on some factor related to developmental rates, such as age at first reproduction, or mutations in a regulatory gene that operates at a critical developmental stage, can have profound consequences for large suites of morphological traits.

Considerations such as these are not formally incorporated into parsimony methods (nor are they a part of other quantitative methods of phylogenetic inference, such as character compatibility or maximum likelihood). This is not to say that they are deemed irrelevant by parsimony advocates. If explicit, objective, and usable guidelines could be developed for incorporating information about developmental programs into phylogenetic analysis, they would presumably be welcomed and used. However, given our present ignorance about such matters, there is little choice but to treat them as a black box, if one is to develop a rigorous and objective methodology for phylogenetic inference. All methodologies are based upon initial assumptions. There is not an alternative to parsimony methods that is free of them. The general objective of all numerically-based methods in systematics is to develop analytical procedures whose premises are clearly stated and open to scrutiny. The important question is whether the assumptions underlying parsimony analysis could lead us seriously astray in attempting to determine the true cladistic relationships among a group of organisms. Unfortunately, we cannot expect to confirm or refute hypotheses of cladistic relationships by direct observation of the speciation events that generate the pattern of cladistic relationships.

What we can observe directly are traits of organisms. In a parsimony analysis, all similar traits shared by two or more taxa are initially hypothesized to be homologous, *i.e.* inherited from a common ancestor. Conflicts in the distribution of these hypothesized homologies among taxa are settled by selecting the branching pattern supported by the largest number of hypothesized homologies. The quantitative precision of this procedure thus depends on the assumption that the features identified as separate "traits" or "characters" can be tallied separately in order to derive a logically well-supported hypothesis of cladistic relationships. If what is "really" a single character has erroneously been coded as several independent characters, this is very likely to influence the branching pattern that will be selected as most parsimonious. I am not aware of any simple, reliable *a priori* tests of the assumption that characters are "cladistically independent". Independence is an initial assumption of the parsimony method, and the validity of the final cladistic hypothesis will depend on the validity of this initial assumption.

These considerations seem particularly important with regard to hypotheses of cladistic relationships among subgroups of *Nomada* because it has been difficult to identify potentially informative characters for cladistic analysis. To the extent that species have been correctly identified, there appears to be considerable *intra*specific variability in a number of the most obvious features of external morphology, such as color patterns, vestiture, and certain aspects of wing venation. It has proven challenging to find two or more presumably independent morphological characters that show the same distribution among species of *Nomada*. Such characters do exist, however. For example, the species of the *vegana* group share a number of distinctive apomorphic features that seem very unlikely to be due to convergent adaptation, since they involve the male mandibles, the postocciput, the pronotum, the penis valves, and the inner dorsal lobe of the gonocoxite. This is the type of list of shared similarities that gives one confidence that one has identified a monophyletic group. Other groups within *Nomada* whose monophyly seems well supported are the *integra* group, the *odontophora* group, the *erigeronis* group, the *bifasciata* group, the *furva* group, and the *trispinosa* group. In other words, many of the terminal branches on the cladograms presented in this paper appear to be monophyletic. Furthermore, as discussed earlier, the monophyly of the genus *Nomada* as defined in this study seems well supported. The identification and characterization of these well-supported monophyletic groups might be considered the

most significant outcome of the cladistic analyses presented here.

The greatest uncertainty concerns the relationships within two large paraphyletic assemblages, the *roberjeotiana* and *ruficornis* groups, and among the major clades of *Nomada* identified in this study. The various resolutions of relationships among these major clades depend heavily upon features of the male genitalia, and in some cases upon decisions about defining alternate states of complex, multistate characters. Furthermore, the polarities of these genitalic characters are often difficult to determine, due to the very different forms of such structures as the gonostyli, penis valves, and gonocoxites in the outgroup taxa as well as within *Nomada*.

In short, there are limits to what can be inferred about cladistic relationships within *Nomada* on the basis of the observed variation in features of external adult morphology. Other potential sources of information do exist. Internal anatomy has not been examined in any serious or comprehensive way, so it is an open question whether phylogenetically informative variation may exist. In my dissections of the female reproductive tracts of nomadine bees (unpublished observations), I have observed that the *Nomada* species I have examined have the Dufour's gland absent or extremely reduced, and this distinguishes them from the other genera I have examined. Some species of *Nomada* have oocytes with a small nipple apically, whereas others do not (Alexander and Rozen, 1987). Host relationships are still poorly documented for *Nomada*, but it is clear that a wide range of hosts are utilized (tabulated in Alexander, 1991), so host choice could conceivably be used as a character in a cladistic analysis. Tengö and Bergström (1979) have documented interesting intra- and interspecific variation in the mandibular gland chemistry of several European species of *Nomada* (and pointed out convergence in the chemistry of male, but not female, mandibular gland contents of *Nomada* and their *Andrena* hosts). Considerable interest is currently being expressed in the promise of DNA analysis as the key to unravelling the phylogeny of all organisms, and *Nomada* of course has DNA. I would encourage the use of any and all of these characters in future phylogenetic studies of *Nomada*. The major drawback to such characters, and the reason they were not incorporated into the present analysis, is simply that the state of each of them is unknown for most of the 800+ species of *Nomada*. Furthermore, it is likely to remain unknown for the foreseeable future, unless an army of researchers should suddenly turn its attention to studying the phylogeny of this largely neglected genus of cleptoparasitic bees. In the meantime, the present analysis is offered as a first approximation.

ACKNOWLEDGMENTS

This research was conducted in partial fulfillment of the requirements for a Ph.D. degree in the field of Entomology at Cornell University. I am particularly indebted to my major professor, George C. Eickwort, who has been a superb advisor, and to the other members of my Special Committee, Richard B. Root and Quentin D. Wheeler. Funding to support the research was provided by Cornell University and by National Science Foundation Dissertation Improvement Grant No. BSR-8714977 to George C. Eickwort and Byron A. Alexander.

It would have been impossible for me to have done this study without the extraordinary cooperation and assistance I received from Maximilian Schwarz and Roy Snelling. In addition to assisting my scientific efforts, both of them welcomed me into their homes and treated me as a friend as well as a colleague. I will always be grateful for their help and advice. Others who provided special assistance and intellectual stimulation were Derek Broemeling, M. C. Day, George Else, Ronald J. McGinley, and Jerome G. Rozen, Jr. E. R. Hoebeke provided the scanning electron micrographs, for which I am most grateful.

A hiatus of about three years separated the version of this study that served as part of my dissertation at Cornell from the present version. During this time, Arturo Roig-Alsina published several important papers on nomadine phylogeny that led me to substantially alter my cladistic analyses. I am especially indebted to him for freely sharing his considerable knowledge of nomadine bees with me. This was also a time when I had the opportunity for numerous stimulating and informative discussions of *Nomada* phylogeny with Charles D. Michener. I am also grateful to him for carefully reading the entire manuscript. I am deeply indebted to Virginia Ashlock for thoroughly checking the lists of species names, especially in the catalog (Alexander and Schwarz, 1994) and trying to insure that literature citations are in a uniform format. Finally, two (more or less) anonymous reviewers carefully picked through the manuscript and uncovered numerous errors of omission or comission. Despite all this help, the sad fact remains that the manuscript probably still contains errors of fact for which I am, of course, ultimately responsible.

The following institutions and individuals have loaned specimens and/or assisted me during visits to their collections: Academy of Natural Sciences of Philadelphia, Don Azuma; American Museum of Natural History, Marjorie Favreau and Jerome G. Rozen, Jr.; Australian National Insect Collection, J. C. Cardale; The Natural History Museum (London, England), George Else; Colorado State University, Howard E. Evans; Cornell University Insect Collection, George C. Eickwort and James K. Liebherr; Hope Entomological Collections, University Museum, Oxford University, Christopher O'Toole; Institute of Biology and Pedology, Vladivostok, N. V. Kurzenko; Maximilian Schwarz personal collection, Ansfelden, Austria; Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Arturo Roig-Alsina; Museum of Comparative Zoology, Harvard University, James M. Carpenter; Natural History Museum of Los Angeles County, Roy Snelling; Snow Entomological Museum, University of Kansas, Robert W. Brooks and Charles D. Michener; South African National Collection of Insects, Connal Eardley; United States National Museum of Natural History, Ronald J. McGinley; University of Colorado Museum, Michael Weissmann and Url Lanham; University of Nebraska State Museum, Brett Ratcliffe; USDA Bee Biology and Systematics Laboratory, Utah State University, Derek Broemeling and Terry Griswold; Zoological Museum of Denmark, Ole Lomholdt; Zoological Museum, University of Helsinki, Olof Biström; Zoological Museum, Munich, Germany, Erich Diller.

LITERATURE CITED

Alexander, B. 1990. A cladistic analysis of the nomadine bees (Hymenoptera: Apoidea). Syst. Entomol. 15: 121-152.

Alexander, B. 1991. *Nomada* phylogeny reconsidered. Jour. Nat. Hist. 25: 315-330.

Alexander, B. and J.G. Rozen , Jr. 1987. Ovaries, ovarioles, and oocytes of parasitic bees. Pan-Pac. Entomol. 63: 155-164.

Alexander, B. A. and Schwarz, M. 1994. A catalog of the species of *Nomada* (Hymenoptera: Apoidea) of the world. Univ. Kansas Sci. Bull. 55: 239-268.

Bischoff, H. 1927. Biologie der Hymenopteren. Berlin, Springer.

Brauns, H. 1930. Neue Bienen aus Süd-Afrika. Konowia 9: 43-54.

Broemeling, D.K. 1988. A revision of the *Nomada* subgenus *Nomadita* of North America (Hymenoptera: Anthophoridae). Pan-Pac. Entomol. 64: 321-344.

Broemeling, D.K., and A.S. Moalif. 1988. A revision of the *Nomada* subgenus *Pachynomada* (Hymenoptera: Anthophoridae). Pan-Pac. Entomol. 64: 201-227.

Brooks, R.W. 1988. Systematics and phylogeny of the anthophorine bees (Hymenoptera: Anthophorinae; Anthophorini). Univ. Kansas Sci. Bull. 53: 436-575.

Cameron, P. 1902. Descriptions of new genera and species of Hymenoptera collected by Major C. G. Nurse at Deesa, Simla, and Ferozepore. Jour. Bombay Nat. Hist. Soc. 14: 419-420.

Cockerell, T.D.A. 1900. Observations on bees collected at Las Vegas, New Mexico, and in the adjacent mountains. Ann. Mag. Nat. Hist. (7)5: 401-416.

Cockerell, T.D.A. 1903a. New American Hymenoptera, mostly of the genus *Nomada*. Ann. Mag. Nat. Hist. (7)12: 200-214.

Cockerell, T.D.A. 1903b. Bees of the genus *Nomada* from California. Proc. Acad. Nat. Sci. Philadelphia 55: 559-579.

Cockerell, T.D.A. 1903c. North American bees of the genus *Nomada*. Proc. Acad. Nat. Sci. Philadelphia 55: 580-614.

Cockerell, T.D.A. 1909. Two new bees. Canadian Entomol. 41: 35-37.

Cockerell, T.D.A. 1911. Bees in the collection of the United States National Museum, 1. Proc. U. S. Natl. Mus. 39: 635-638.

Cockerell, T.D.A. 1916. Some Neotropical parasitic bees. Entomol. News 27: 208-210.

Cockerell, T.D.A. 1919. Bees in the collection of the United States National Museum, 3. Proc. U. S. Natl. Mus. 55: 167-221.

Cockerell, T.D.A. 1928. Bees collected in Siberia in 1927. Ann. Mag. Nat. Hist. (19)1: 345-361.

Cockerell, T.D.A. 1931. The bees of Australia. Australian Zool. 7: 34-54.

Cockerell, T.D.A., and E. Atkins. 1902. On the bees of the family Nomadidae of Ashmead. Ann. Mag. Nat. Hist. (7)10: 42-46.

Cresson, E.T. 1863. On the North American species of the genus *Nomada*. Proc. Entomol. Soc. Philadelphia 2: 280-312.

Cresson, E.T. 1872. Hymenoptera Texana. Trans. American Entomol. Soc. 4: 153-292.

Cresson, E.T. 1878. Descriptions of new North American Hymenoptera in the collection of the American Entomological Society. Trans. American Entomol. Soc. 7: 61-136.

Curtis, J. 1832. British Entomology, Vol. 9, folio 419. London: John Cumberland.

Dalla Torre, C.G. de. 1896. Catalogus Hymenopterorum, v. X. Apidae (Anthophila). Lipsiae. 643 pp.

Darwin, C. 1859. The Origin of Species. London: John Murray.

Day, M.C. 1979. The species of Hymenoptera described by Linnaeus in the genera *Sphex, Chrysis, Vespa, Apis* and *Mutilla*. Biol. Jour. Linn. Soc. London 12: 45-84.

Eardley, C., and M. Schwarz. 1991. The Afrotropical species of *Nomada* Scopoli (Hymenoptera: Anthophoridae). Phytophylactica 23: 17-27.

Ebmer, A.W. 1976. Liste der Mitteleuropaischen *Halictus*- und *Lasioglossum*-Arten. Linzer Biol. Beitr. 8: 393-405.

Eickwort, G.C. 1988. Distributional patterns and biology of West Indian sweat bees (Hymenoptera: Halictidae), pp. 231-253. *In*: Liebherr, J.K. (ed.) Zoogeography of Caribbean Insects. Ithaca, N.Y.: Comstock Publishing Associates, Cornell University Press.

Eickwort, G.C., and J. Abrams. 1980. Parasitism of sweat bees in the genus *Agapostemon* by cuckoo bees in the genus *Nomada* (Hymenoptera: Halictidae, Anthophoridae). Pan-Pac. Entomol. 56: 144-152.

Evans, D.L. 1972. A revision of the subgenus *Holonomada* of the genus *Nomada* (Hymenoptera: Anthophoridae). Wasmann Jour. Biol. 30: 1-34.

Eversmann, 1852. Fauna Hymenopterologica Volgo-Uralensis (continuatio). Bull. Soc. Imp. Nat. Moscou 25: 1-137.

Fabricius, J.C. 1775. Systema Entomologiae. Flensburgi et Lipsiae.

Fabricius, J.C. 1793. Entomologica Systematica, v. 2. Hafniae.

Fabricius, J.C. 1805. Systema Piezatorum. Brunsvigae.

Farris, J.S. 1969. A successive approximations approach to character weighting. Syst. Zool. 18: 374-385.

Farris, J.S. 1983. The logical basis of phylogenetic analysis, pp. 7-36. *In*: Platnick, N.I., and V.A. Funk (eds.), Advances in Cladistics 2. Proceedings of the second meeting of the Willi Hennig Society. New York: Columbia University Press.

Farris, J.S. 1988. Hennig86, documentation for Version 1.5. Port Jefferson, New York.

Friese, H. 1888. Die Schmarotzerbienen und ihre Wirte. Zool. Jahrb., Syst. 3: 847-870.

Friese, H. 1923. Die Europäischen Bienen. Berlin und Leipzig.

Gould, S.J. 1977. Ontogeny and Phylogeny. Cambridge, Mass: Harvard University Press.

Hennig, W. 1966. Phylogenetic Systematics. Urbana, Ill.: University of Illinois Press.

Herrich-Schäffer, G.A.W. 1839. Auseinandersetzung der europäischen Arten einiger Bienengattungen, Gattung *Nomada*. Zeitschr. Entomol. 1: 267-288.

Hirashima, Y. 1960. Bees of the Amami islands II (Hymenoptera, Apoidea). Mushi 33: 53-62.

Hirashima, Y. 1972. Comparative studies on the orientation of pupa in the nests of solitary bees and wasps. Sci. Bull. Fac. Agr. Kyushu Univ. 26: 27-45. (In Japanese, cited in Maeta et al., 1987.)

Holmberg, E.L. 1886. Sobre apidos nomadas de la Republica Argentina. An. Soc. Cient. Argentina 22: 231-240, 272-286.

Hurd, P.D., Jr. 1979. Apoidea, pp. 1741-2209. *In*: Krombein, K.V., P.D. Hurd, Jr., D.R. Smith, and B.D. Burks (eds.), Catalog of Hymenoptera in America North of Mexico, Vol. 2. Washington, D.C.: Smithsonian Institution Press.

Kirby, W. 1802. Monographia Apum Angliae, Vol. 2. Ipswich [London].

Knerer, G. 1968. Zur Bienenfauna Niederösterreichs: Die Unterfamilie Halictinae. Zool. Anz. 181: 82-117.

Kocourek, M. 1966. Prodromus der Hymenopteren der Tschechoslowakei, Pars 9: Apoidea, 1. Acta Faun. Entomol. Mus. Nat. Pragae 12: 1-122.

Kohl, F.F. 1905. Hymenopteren. *In*: Penther, A. and E. Zederbauer (eds.), Ergebnisse einer naturwissenschaftlichen Reise zum Erdschias-Dagh (Kleinasien). Ann. K. K. Naturhist. Hofmus. 20: 220-246.

Linnaeus, C. 1758. Systema Naturae, ed. 10. Holmiae.

Linnaeus, C. 1767. Systema Naturae, ed. 12, 1 (2): 533-1327.

Linsley, E.G., and J.W. MacSwain. 1955. The habits of *Nomada opacella* Timberlake with notes on other species (Hymenoptera: Anthophoridae). Wasmann Jour. Biol. 13: 253-276.

Linsley, E.G., and C.D. Michener. 1939. A generic revision of the North American Nomadidae. Trans. American Entomol. Soc. 65: 265-305.

Maddison, W.P., M.J. Donoghue, and D.R. Maddison. 1984. Outgroup analysis and parsimony. Syst. Zool. 33: 83-103.

Maeta, Y., N. Kubota, and S.F. Sakagami. 1987. *Nomada japonica* as a thelytokous cleptoparasitic bee, with notes on egg size and egg complement in some cleptoparasitic bees. Kontyu 55: 21-31.

Masuda, H. 1940. Biological notes on *Eucera difficilis* Pérez and its parasitic bee, *Nomada japonica* Smith, with description of a gy-

nandromorphic *Eucera*. Kontyu 14: 45-60. (In Japanese, cited in Maeta et al., 1987.)
Mayr, E. 1942. Systematics and the Origin of Species. New York: Columbia University Press.
McGinley, R.J. 1986. Studies of Halictinae (Apoidea: Halictidae), I: Revision of New World *Lasioglossum* Curtis. Smithson. Contrib. Zool., No. 429, 294 pp.
Michener, C.D. 1944. Comparative external morphology, phylogeny, and a classification of the bees (Hymenoptera). Bull. American Mus. Nat. Hist. 82: 151-326.
Michener, C.D. 1974. The Social Behavior of the Bees. Cambridge, Mass.: Harvard University Press.
Michener, C.D. 1979. Biogeography of the bees. Ann. Missouri Bot. Gard. 66: 277-347.
Mickevich, M. 1982. Transformation series analysis. Syst. Zool. 31: 461-478.
Mitchell, T.B. 1962. Bees of the Eastern United States, II. North Carolina Agr. Expt. Sta. Tech. Bull. 152: 1-557.
Mocsáry, A. 1883. Hymenoptera nova europaea et exotica. Magy. Akad. Termész. Értek 13: 1-72.
Mocsáry, A. 1894. E Fauna Apidarum Hungariae. Termes. Füzetek 17: 34-37.
Morawitz, F. 1870. Beitrag zur Bienenfauna Russlands. Hor. Soc. Entomol. Ross. 7: 305-333.
Moure, J.S. 1960. Notes on the types of the neotropical bees described by Fabricius (Hymenoptera: Apoidea). Studia Entomologica 3: 97-160.
Nelson, G. 1972. Phylogenetic relationship and classification. Syst. Zool. 21: 227-231.
Olivier, G.A. 1811. Encyclopédie Méthodique. Dictionnaire des Insectes, v. 8. Paris and Liège.
Parker, F.D. and G.E. Bohart. 1982. Notes on the biology of *Andrena (Callandrena) helianthi* Robertson (Hymenoptera: Andrenidae). Pan-Pac. Entomol. 58: 111-116.
Parker, F.D. and T. Griswold. 1982. Biological notes on *Andrena (Callandrena) haynesi* Viereck and Cockerell (Hymenoptera: Andrenidae). Pan-Pac. Entomol. 58: 284-287.
Pérez, J. 1884. Contribution a la Faune des Apiaires de France. Act. Soc. Linn. Bordeaux 37: 205-380.
Perkins, R.C.L. 1919. The British species of *Andrena* and *Nomada*. Trans. Entomol. Soc. London 1919: 218-320.
Pittioni, B. 1952. Die *Nomada*-Arten der Alten Welt: Bestimmungstabelle der Mannchen. Ann. Naturh. Mus. Wien 59: 221-291.
Plateaux-Quénu, C., and L. Plateaux. 1986. Alternance de generations chez *Evylaeus villosulus* (K.) (Hym., Halictinae). Act. Coll. Ins. Soc. 3: 73-82.
Robertson, C. 1893. Notes on bees, with descriptions of new species. Trans. American Entomol. Soc. 20: 245-248, 273-276.
Robertson, C. 1897. North American bees—descriptions and synonyms. Trans. Acad. Sci. St. Louis 7: 315-356.
Robertson, C. 1903. Synopsis of Nomadinae. Canadian Entomol. 35: 172-179.
Rodeck, H.G. 1945. Two new subgenera of *Nomada* Scopoli (Hym.: Apoidea). Entomol. News 56: 179-181.
Rodeck, H.G. 1947. *Laminomada*, new subgenus of *Nomada* (Hym.: Apoidea). Ann. Entomol. Soc. America 40: 266-270.
Rohwer, S.A. 1911. A new genus of nomadine bees. Entomol. News 22: 24-27.
Roig-Alsina, A. 1989. The tribe Osirini, its scope, classification and revisions of the genera *Parepeolus* and *Osirinus* (Hymenoptera, Apoidea, Anthophoridae). Univ. Kansas Sci. Bull. 54: 1-23.
Roig-Alsina, A. 1990. *Coelioxoides* Cresson, a parasitic genus of Tetrapediini (Hymenoptera, Apoidea). Jour. Kansas Entomol. Soc. 63: 279-287.
Roig-Alsina, A. 1991. Cladistic analysis of the Nomadinae s. str. with description of a new genus (Hymenoptera: Anthophoridae). Jour. Kansas Entomol. Soc. 64: 23-37.
Roig-Alsina, A. and Michener, C.D. 1993. Studies of the phylogeny and classification of long-tongued bees (Hymenoptera: Apoidea). The University of Kansas Science Bulletin 55 (4): 124-162.
Rozen, J.G., Jr. 1966. The larvae of the Anthophoridae (Hymenoptera; Apoidea), Part 2, The Nomadinae. American Mus. Novitates 2244: 1-38.
Rozen, J.G., Jr. 1977. Immature stages of and ethological observations on the cleptoparasitic bee tribe Nomadini (Hymenoptera, Anthophoridae). American Mus. Novitates 2638: 1-16.
Rozen, J.G., Jr. 1991. Evolution of cleptoparasitism in anthophorid bees as revealed by their mode of parasitism (Hymenoptera: Apoidea). American Mus. Novitates 3029: 1-36.
Rozen, J.G., Jr., K.R. Eickwort, and G.C. Eickwort. 1978. The bionomics and immature stages of the cleptoparasitic bee genus *Protepeolus* (Anthophoridae, Nomadinae). American Mus. Novitates 2640: 1-24.
Say, T. 1837. Descriptions of new species of North American Hymenoptera, and observations on some already described. Boston Jour. Nat. Hist. 1: 361-416.
Schilling, P.S. 1849. Die sogenannten Einsiedler-Bienen Schlesiens. Arbeit. Schles. Ges. Vaterl. Kultur 1849: 98-104.
Schmiedeknecht, H.L.O. 1882. Genus *Nomada* Fab. (sic), pp. 1-249, *In*: Apidae Europaeae, Tomus I. Gumperdae et Berolini.
Schwarz, M. 1966. Beitrag zur Subfamilie Nomadinae (Hymenoptera, Apoidea). Polskie Pismo Entomol. 36: 383-394.
Schwarz, M. 1967. Die Gruppe der *Nomada cinctiventris* Fr. (= *stigma* auct. nec F.) (Hymenoptera, Apoidea). Polskie Pismo Entomol. 37: 263-339.
Schwarz, M. 1974. Zwei neue Arten aus der Gruppe der *Nomada fuscicornis* Nyl. und Beschreibung des noch unbekannten Männchens der *Nomada rufoabdominalis* Schwarz (Hym., Apidae). Polskie Pismo Entomol. 44: 257-266.
Schwarz, M. 1977. Ergebnisse der Untersuchungen der von J. Pérez 1895 in "Espéces nouvelles de Mélliferes de Barbarie" beschriebenen *Nomada*-Arten und Beschreibung von vier neuen Arten (Hymenoptera, Apoidaea [sic]). Mitt. Münchner Entomol. Ges. 66: 39-79.
Schwarz, M. 1981. 1. Beitrag zur *Nomada*-Fauna der Türkei (Hymenoptera: Apoidea). Entomofauna 2: 357-414.
Schwarz, M. 1986. Zur Kenntnis der Gattung *Nomada* Scopoli, 2 (Hymenoptera, Apoidea). Entomofauna 7: 453-467.
Schwarz, M. 1987. Neue *Nomada*-Arten aus der UdSSR 1 (Hymenoptera, Apoidea). Entomofauna 8: 453-471.
Schwarz, M. 1988. Revision einiger von T.D.A. Cockerell beschriebenen *Nomada*-Arten der Paläarktis (Hymenoptera, Apoidea). Entomofauna 9: 381-387.
Schwarz, M. 1989. Zur Kenntnis Afrikanischer *Nomada*-Arten (Hymenoptera, Apoidea). Linzer Biol. Beitr. 21: 303-313.
Schwarz, M. 1990. Beitrag zur Kenntnis orientalischer *Nomada*-Arten (Hymenoptera, Apidae, Nomadinae). Entomofauna, Supplement 5: 1-56.
Scopoli, J.A. 1770. Annus Historico Naturalis, v. 4.
Sharkey, M.J. 1989. A hypothesis-independent method of character weighting for cladistic analysis. Cladistics 5: 63-86.
Smith, F. 1846. Bees of Great Britain. Zoologist 4: 267-288.
Smith, F. 1854. Catalogue of Hymenoptera in the Collection of the British Museum, v. 2, pp. 199-465.
Smith, F. 1876. Catalogue of the British Bees in the Collection of the British Museum. London: British Museum (Natural History).
Snelling, R.R. 1986. Contributions toward a revision of the New World nomadine bees: a partitioning of the genus *Nomada* (Hymenoptera: Anthophoridae). Contrib. Sci., Los Angeles Co. Nat. Hist. Mus. No. 376: 1-32.
Snelling, R.R., and J.G. Rozen, Jr. 1987. Contributions toward a revision of the New World nomadine bees, 2: The genus *Melanomada* (Hymenoptera: Anthophoridae). Contrib. Sci., Los Angeles Co. Nat. Hist. Mus. No. 384: 1-12.
Sokal, R.R. and P.H.A. Sneath. 1963. The Principles of Numerical Taxonomy. San Francisco: W.H. Freeman & Co.
Stöckhert, E. 1941. Über die Gruppe der *Nomada zonata* Panz. (Hym. Apid.). Mitt. Münchner Entomol. Ges. 31: 1072-1122.
Stöckhert, E. 1943. Über die Gruppe der *Nomada furva* Panz. (Hym. Apid.). Deutsch. Entomol. Zeitschr. 1943: 89-126.

Stöckhert, E. 1930. *Nomada* F. (sic), pp. 986-1053. *In*: Schmiedeknecht (ed.), 1930. Die Hymenopteren Nord- und Mitteleuropas. Jena: Fischer.
Stoeckhert, F.K. 1932. Die Bienen Frankens. Beiheft, Deutsch. Entomol. Zeitschr., 1932: i-vii + 1-294.
Swenk, M.H. 1913. Studies of North American bees. I. Family Nomadidae. Univ. Stud. (Lincoln, Nebraska) 12: 1-113.
Swenk, M.H. 1915. Studies of North American bees. III. Families Nomadidae and Stelididae. Univ. Stud. (Lincoln, Nebraska) 15: 155-193.
Swofford, D.L. 1993. PAUP: Phylogenetic Analysis Using Parsimony, Version 3.1. Computer program and instruction manual distributed by the Illinois Natural History Survey.
Tengö, J., and G. Bergström. 1977. Cleptoparasitism and odor mimetism in bees: Do *Nomada* males imitate the odor of *Andrena* females? Science 196: 1117-1119.
Tsuneki, K. 1973. Studies on *Nomada* of Japan. Etizenia 66 (1,2): 1-141.
Tsuneki, K. 1975. Corrigenda and addenda to the studies on *Nomada* (Hymenoptera, Apidae) of Japan. Kontyu 43: 463-477.
Tsuneki, K. 1976a. Additions to the *Nomada*-fauna of Japan (Hymenoptera, Apidae). Kontyu 44: 150-158.
Tsuneki, K. 1976b. New species of the genus *Nomada* Scopoli (Hymenoptera, Apidae) in Japan. Kontyu 44: 49-64.
Tsuneki, K. 1986. New species and subspecies of the aculeate Hymenoptera from East Asia, with some synonyms, specific remarks and distributional data. Spec. Publ. Japan Hymen. Assoc. 32: 1-60.
Warncke, K. 1982. Zur Systematik der Bienen—Die Unterfamilie Nomadinae (Hymenoptera, Apidae). Entomofauna 3: 97-126.
Westrich, P. 1989. Die Wildbienen Baden-Wurttembergs (2 vol.). Stuttgart: Eugen Ulmer.
Wheeler, Q.D. 1986. Character weighting and cladistic analysis. Syst. Zool. 35: 102-109.
Wiley, E.O. 1981. Phylogenetics, the theory and practice of phylogenetic systematics. New York: John Wiley & Sons.
Yasumatsu, K. 1938. Die von Professor Dr. S. Matsumura beschriebenen Kuckucksbienen aus Japan (Ernster Beitrag zur Kenntnis die *Nomada*-Arten Japans). Ins. Matsum. 13: 39-40.

APPENDIX

Outgroup taxa examined for the quantitative cladistic analyses. Tribes are as defined in Roig-Alsina (1991) and Roig-Alsina and Michener (1993).

Tribe Ammobatini: *Oreopasites vanduzeei* Cockerell, *Pasites maculatus* Jurine.
Tribe Ammobatoidini: *Ammobatoides abdominalis* (Eversmann), *Holcopasites calliopsidis* (Linsley), *Holcopasites insoletus* (Linsley).
Tribe Biastini: *Biastes brevicornis* (Panzer), *Biastes emarginatus* (Schenck), *Neopasites cressoni* Crawford, *Neopasites mojavensis* (Linsley).
Tribe Brachynomadini: *Brachynomada* sp., *Kelita chilensis* (Friese), *Melanomada grindeliae* (Cockerell).
Tribe Caenoprosopidini: *Caenoprosopis crabronina* Holmberg.
Tribe Epeolini: *Epeolus floridensis* Mitchell, *Odyneropsis gertschi* Michener, *Rhinepeolus rufiventris* (Friese), *Rhogepeolus bigibbosus* Moure, *Thalestria spinosa* (Fabricius), *Triepeolus lunatus* (Say), *Trophocleptria bifasciata* (Cresson).
Tribe Hexepeolini: *Hexepeolus mojavensis* Linsley & Michener, *Hexepeolus rhodogyne* Linsley & Michener (female only).
Tribe Neolarrini: *Neolarra californica* Michener, *Neolarra verbesinae* (Cockerell).
Tribe Townsendiellini: *Townsendiella californica* Michener, *Townsendiella rufiventris* Linsley.

ANNOUNCEMENT

The *University of Kansas Science Bulletin* (continuation of the *Kansas University Quarterly*) is an outlet for scholarly scientific investigations carried out at the University of Kansas or by University faculty and students. Since its inception, volumes of the *Bulletin* have been variously issued as single bound volumes, as two or three multi-paper parts or as series of individual papers. Issuance is at irregular intervals, with each volume prior to volume 50 approximately 1000 pages in length. Effective with volume 50, page size has been enlarged, reducing the length of each volume to about 750 pages.

The supply of all volumes of the *Kansas University Quarterly* is now exhausted. However, most volumes of the University of Kansas Science Bulletin are still available and are offered, in exchange for similar publications, to learned societies, colleges and universities and other institutions, or may be purchased at $30.00 per volume. Where some of these volumes were issued in parts, individual parts are priced at the rate of 3 cents per page. Current policy, initiated with volume 46, is to issue individual papers as published. Such separata may be purchased individually at the rate of 7 cents per page, with a minimum charge of $1.50 per separate. Subscriptions for forthcoming volumes may be entered at the rate of $30.00 per volume. All communications regarding exchanges, sales and subscriptions should be addressed to the Exchange Librarian, University of Kansas Libraries, Lawrence, Kansas 66045.

Individual papers for personal use by investigators are available for most recent and many older issues of the Bulletin. Such requests should be directed to the author or to the relevant Museum or Department of the University of Kansas.

The International Standard Serial Number of this publication is US ISSN 0022-8850.

Editor
Charles D. Michener

Editorial Board
Meredith Lane, *Chairman*
James S. Ashe
George W. Byers
Christopher Haufler
Norman A. Slade

MCZ LIBRARY HARVARD

THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. 55, No. 7, pp. 239-270 March 30, 1994

A Catalog of the Species of *Nomada* (Hymenoptera: Apoidea) of the World

BYRON A. ALEXANDER[1] AND MAXIMILIAN SCHWARZ[2]

TABLE OF CONTENTS

Abstract 239
Introduction 240
Catalog 240
gigas group p. 240, *integra* group p. 240, *adducta* group p. 241, *vincta* group p. 241, *odontophora* group p. 241, *vegana* group p. 241, *roberjeotiana* group p. 242, *erigeronis* group p. 243, *rodecki* p. 244, *ruficornis* group p. 244 *armata* group p. 253, *belfragei* group p. 254, *superba* group p. 254, *basalis* group p. 255, *bifasciata* group p. 255, *trispinosa* group p. 256, *furva* group p. 256, *Nomada* species incertae sedis p. 257
Literature Cited 259
Index of Species Names 259

ABSTRACT

A catalog of the species of *Nomada* of the world is presented. Species are arranged according to the species groups recognized in Alexander's (1994) revision. The combination *Nomada maculipennis* (Cameron, 1902), which was created when Cockerell (1931) correctly synonymized *Lamproapis* Cameron 1902 with *Nomada*, makes *Nomada maculipennis* Friese (in Friese and Schulthess, 1923) a secondary junior homonym. *Nomada koreana* Tsuneki 1986 is a primary junior homonym of *Nomada koreana* Cockerell 1926, *N. bimaculata* Eversmann 1852 is a primary junior homonym of *N. bimaculata* Schilling 1849, and *N. syriaca* Friese 1920 is a primary junior homonym of *N. syriaca* Dusmet 1915. *Nomada cypricola* Mavromoustakis 1957 is a primary junior homonym of *Nomada cinnabarina* var. *cypricola* Mavromoustakis 1955. No new names are proposed at this time, pending determination of whether synonyms already exist for the junior homonyms. *Nomada mimus* (Cockerell), *Nomada hakusana hakusana* Tsuneki, and *Nomada hakusana momoglonis* Tsuneki are proposed as new combinations.

[1] DEPARTMENT OF ENTOMOLOGY AND SNOW ENTOMOLOGICAL MUSEUM, SNOW HALL, UNIVERSITY OF KANSAS, LAWRENCE, KANSAS 66045-2119 USA.
[2] KONSULENT FÜR WISSENSCHAFT DER OÖ. LANDESREGIERUNG, EIBENWEG 6, A-4052 ANSFELDEN, AUSTRIA

INTRODUCTION

The last comprehensive list of species of the large, nearly cosmopolitan cleptoparasitic bee genus *Nomada* was included in Volume X of Dalla Torre's (1896) *Catalogus Hymenopterorum*. Numerous new species have been described since then, and many new synonymies have been proposed; so the time for an updated list is long overdue. Schwarz has been clarifying the nomenclature and describing new species of Old World *Nomada* for many years, and has developed a worldwide catalog in the form of a computerized database. When Alexander began his study of phylogenetic relationships among species-groups within *Nomada* (Alexander, 1994), he drew heavily upon Schwarz's work in developing a provisional list of species that should be assigned to each of the groups he recognized in his revision. The present catalog thus combines the results of a collaboration that has developed over a period of several years. A great deal of species-level taxonomy remains to be done within *Nomada*. Our primary objective is to make the work of future revisers easier and to minimize the problem of homonymy by compiling in one place all of the published names and synonyms known to us.

Although the species group names used here are not intended to have any formal nomenclatural status, lists of included species are presented so that the proposed composition of the groups will be as unambiguous as possible. Descriptions of the species groups are in Alexander (1994). Synonyms are listed according to the most recently published treatments. A few cases of previously unrecognized homonyms were detected. These homonyms are listed together in the Abstract to this paper for the benefit of future revisers, but no new names are proposed, pending resolution of the status of the existing names (it is quite possible that the junior homonyms already have available synonyms). For species originally described in a genus other than *Nomada*, the name of the genus in which the species was originally placed is indicated in brackets. In the lists of geographic distributions, U.S. = United States of America.

CATALOG

gigas group

gigas Friese, 1905. Zeitschr. Syst. Hymen. Dipt. 5: 19. South Africa, Cape Province.

kobrowi Brauns, 1912. Deutsche Entomol. Zeitschr. 1912: 68.

gigantea Friese, incorrect spelling *in* Brauns, 1930. Konowia 9: 43.

integra group

cinctiventris group, Schwarz, 1967: 263. (*integra* Brullé is a senior synonym of *cinctiventris* Friese; synonymy in Schwarz, 1986, Entomofauna 7: 461-462).

argentata Herrich-Schäffer, 1839. Zeitschr. Entomol. 1: 276. Central and eastern Europe.

atrata Smith, 1846. Zoologist 4: 1568.

brevicornis Schmiedeknecht, 1882. Apidae Europaeae 1: 241.

beaumonti Schwarz, 1967. Polskie Pismo Entomol. 37: 286. Central and southern Europe, northwest Africa (Tunisia, Algeria).

serricornis Pérez, 1884. Act. Soc. Linn. Bordeaux. 37: 370 (male, not female).

carthaginensis Dusmet, 1932. Eos 8: 232. Northwest Africa (Tunisia, Algeria).

caspia Morawitz, 1895. Hor. Soc. Entomol. Ross. 29: 51. Greece, Turkey, Lebanon, Israel.

graeca Schwarz, 1967. Polskie Pismo Entomol. 37: 289.

facilis Schwarz, 1967. Polskie Pismo Entomol. 37: 291. Central and southeastern Europe.

glaberrima Schmiedeknecht, 1882; Apidae Europaeae 1: 246. Southeastern Europe to Lebanon and Syria.

graja Mocsáry, 1883. Magy. Akad. Termész. Értek. 13: 68.

integra integra Brullé, 1832. Expédition Scientifique de Morée, Zool. II, 3(2): 347. Widespread in Europe, from Finland and England south to Spain & Bulgaria.

ferruginata var. *cinctiventris* Friese, 1921. Deutsche Entomol. Zeitschr. 1920: 253.

ferruginata auct. (nec Linnaeus, 1767).

germanica Fabricius, 1805 (nec Panzer, 1799). Systema Piezatorum, p. 394.

stigma auct. (nec Fabricius, 1805).

integra imperfecta Schwarz, 1967. Mediterranean Region (Tunisia, Algeria, Israel).

cinctiventris ssp. *imperfecta* Schwarz, 1967. Polskie Pismo Entomol. 37: 282.

integra nigra Schwarz, 1967. Mediterranean Region (Italy, Balkan Peninsula).

cinctiventris ssp. *nigra* Schwarz, 1967. Polskie Pismo Entomol. 37: 280.

ortegai Dusmet, 1915. Mem. R. Soc. Española Hist. Nat. 8 (Mem. 7): 328. Morocco.

pallispinosa Schwarz, 1967. Polskie Pismo Entomol. 37: 294. Greece, Italy, Turkey, Israel, and southwest Asia.

pleurosticta Herrich-Schäffer, 1839. Zeitschr. Entomol. 1: 276, Central and southern Europe, Turkey, Tunisia.

bicolor Radoszkowski, 1876. Hor. Soc. Entomol. Ross. 12: 95.

ferruginata var. *major* Morawitz, 1872. Verh. Zool. Bot. Ges. Wien 22: 383.

morawitzi Pérez, 1884. Act. Soc. Linn. Bordeaux 37: 370.

rubiginosa Pérez, 1884. Act. Soc. Linn. Bordeaux 37: 372. France, Spain, Tunisia, Israel.

rubricollis Schwarz, 1967. Polskie Pismo Entomol. 37: 299. Greece, Turkey, Syria, Israel, southern Russia (Derbent).

stigma cypricola Mavromoustakis, 1955. Mediterranean Region (Cyprus).

cinnabarina var. *cypricola* Mavromoustakis, 1955. Ann. Mag. Nat. Hist. (12)8: 97.

stigma obscurata Schmiedeknecht, 1882. Mediterranean Region (Greece).

cinnabarina var. *obscurata* Schmiedeknecht, 1882. Apidae Europaeae 1: 239.

stigma stigma Fabricius, 1805. Systema Piezatorum, p. 393. Throughout Europe, North Africa, western Asia.

austriaca Schmiedeknecht, 1882. Apidae Europaeae 1: 238.

cinnaberina Morawitz, 1871. Hor. Soc. Entomol. Ross. 7: 330.

cinnabarina Morawitz, 1872. Verh. Zool. Bot. Ges. Wien 22: 384.

cinnabarina var. *slovakica* Mavromoustakis, 1955. Ann. Mag. Nat. Hist. (12)8: 97.

stigma villipes Stöckhert, 1930. Central Europe (Germany [Bamberg]).

cinnabarina ssp. *villipes* Stöckhert 1930, *In* Schmiedeknecht. Die Hymenopteren Nord- und Mitteleuropas, p. 1022.

thersites Schmiedeknecht, 1882. Apidae Europaeae 1: 227. Czechoslavakia, Russia, Cyprus, Israel.

maculiscapa Pérez, 1902. Proc.-Verb. Soc. Linn. Bordeaux 57: lxiii.

tridentirostris Dours, 1873. Rev. Mag. Zool. (3)1: 309. Algeria, France, Sicily.

amblystoma Pérez, 1884. Act. Soc. Linn. Bordeaux 37: 376.

cyphognatha Pérez, 1884. Act. Soc. Linn. Bordeaux 37: 374.

adducta group

Nomada subgenus *Asteronomada* Broemeling, 1988. Pan-Pac. Entomol. 64: 336-338. Type species: *Nomada adducta* Cresson, 1878; original designation.

adducta Cresson, 1878. Trans. American Entomol. Soc. 7: 73. Central and western U.S.
brewsterae Broemeling, 1988. Pan-Pac. Entomol. 64: 340. Southwestern U.S. (west Texas).
durangoae Broemeling, 1988. Pan-Pac. Entomol. 64: 341. Northern Mexico (Durango).
portalensis Broemeling, 1988. Pan-Pac. Entomol. 64: 342. Southwestern U.S. (Arizona, New Mexico, west Texas).

vincta group

Nomada subgenus *Pachynomada* Rodeck, 1945, Entomol. News 56: 180. Type species: *Nomada vincta* Say, 1837; original designation.

asteris Swenk, 1913. Univ. Stud. (Lincoln, Nebraska) 12: 89. Central U.S. (Kansas).
aztecorum aztecorum Cockerell, 1903. Ann. Mag. Nat. Hist. (7)12: 211. Central Mexico.
aztecorum pratensis Cockerell, 1919. Proc. U.S. Natl. Mus. 55: 180. Northwestern Mexico.
besseyi Swenk, 1913; Univ. Stud. (Lincoln, Nebraska) 12: 85. Eastern and central U.S.
bohartorum Moalif, 1988. *In:* Broemeling and Moalif, 1988. Pan-Pac. Entomol. 64: 220. Western Mexico.
dreisbachorum Moalif, 1988. *In:* Broemeling and Moalif, 1988. Pan-Pac. Entomol. 64: 222. Central Mexico.
saltillo Broemeling, 1988. *In:* Broemeling and Moalif, 1988. Pan-Pac. Entomol. 64: 214. Northern Mexico.
suffossa Cockerell, 1922. Proc. U.S. Natl. Mus. 60: 16. Central Mexico.
tepoztlan Moalif, 1988. *In:* Broemeling and Moalif, 1988. Pan-Pac. Entomol. 64: 221. Central Mexico.
utahensis Moalif, 1988. *In:* Broemeling and Moalif, 1988. Pan-Pac. Entomol. 64: 215. Western U.S.
victrix Cockerell, 1911. Proc. U.S. Natl. Mus. 39: 657. South Texas to central Mexico.
vincta Say, 1837. Boston Jour. Nat. Hist. 1: 401. Eastern and central U.S.
  vincta heterochroa Cockerell, 1921. American Mus. Novitates 24: 1.
vitticollis Cresson, 1878. Trans. American Entomol. Soc. 7: 78. Eastern Mexico.
zebrata Cresson, 1878. Trans. American Entomol. Soc. 7: 73. Central and southwestern U.S.

odontophora group

Acanthonomada Schwarz, 1966. Polskie Pismò Entomol. 36: 383. Type species: *Nomada odontophora* Kohl, 1905; original designation.
Nomada subgenus *Acanthonomada* Warncke, 1982. Entomofauna 3: 103.

argentea (Schwarz), 1966. Polskie Pismo Entomol. 36: 387. Turkey. (type locality: Tarsus). [*Acanthonomada*].
moricei Friese, 1899. Entomol. Nachr. 25: 286. Syria.
odontophora Kohl, 1905. Ann. K. K. Naturhist. Hofmus. 20: 245. Turkey. (type locality: Erdschias Dag).

vegana group

Cephen Robertson, 1903. Canadian Entomol. 35: 174, 176. Type species: *Nomada texana* Cresson, 1872; original designation and monobasic.
Hypochrotaenia subgenus *Aphelonomada* Snelling, 1986. Contrib. Sci. Los Angeles Co. Nat. Hist. Mus. 376: 9-13. Type species: *Nomada cruralis* Moure, 1960; original designation and monobasic.
Hypochrotaenia Holmberg, 1886. An. Soc. Cient. Argentina 22: 273. Type species: *Hypochrotaenia parvula* Holmberg, 1886; original designation and monobasic.
Nomada subgenus *Micronomada* Cockerell & Atkins, 1902. Ann. Mag. Nat. Hist. (7)10: 44. Type species: *Nomada modesta* Cresson, 1863; original designation.
Nomadosoma Rohwer, 1911. Entomol. News 22: 24. Type species: *Pasites pilipes* Cresson, 1865; original designation and monobasic.
Polybiapis Cockerell, 1916. Entomol. News 27: 208. Type species: *Polybiapis mimus* Cockerell, 1916; original designation.

Species names preceded by a question mark represent those for which we have seen no specimens, but which we infer to belong to this group on the basis of the original descriptions and geographic ranges.

?*abnormis* Ducke, 1912. Zool. Jahrb. Abt. Syst. Geogr. Biol. Tiere 34: 104. South America (Brazil).
advena Smith, 1860. Jour. Entomol. 1: 82. South America (Chile or Colombia?)
amorphae Swenk, 1913. Univ. Studies (Lincoln, Nebraska) 12: 108. West-central U.S. (Nebraska, Colorado).
arenicola Swenk, 1913. Univ. Studies (Lincoln, Nebraska) 12: 107. Central U.S. (Nebraska).
bicellularis Ducke, 1908. Rev. d'Entomol. 27: 36. South America (Argentina, Brazil, Paraguay).
  parvula (Holmberg), 1886 (nec Lucas, 1846; nec De Stefani, 1855). An. Soc. Cient. Argentina 22: 273. [*Hypochrotaenia*]. Preoccupied.
bonaerensis Holmberg, 1886. An. Soc. Cient. Argentina 22: 238. South America (Argentina).
carcaranensis Cockerell, 1917. Ann. Mag. Nat. Hist. (8)20: 236. South America (Argentina).
costalis Brèthes, 1909. An. Mus. Nac. Buenos Aires 12: 249. South America (Argentina).
costaricensis Schrottky, 1920. Rev. Museu Paulista 12: 219. Central America (Costa Rica).
crucis Cockerell, 1903. Ann. Mag. Nat. Hist. (7)12: 212. Southwestern U.S.
cubensis Cresson, 1865. Proc. Entomol. Soc. Philadelphia 4: 180. Cuba.
fervida Smith, 1854. Catalogue of the Hymenoptera in the Collection of the British Museum, v. 2, p. 247. Southeastern U.S.
  crassula Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 610.
?*flaviceps* Cresson, 1865. Proc. Entomol. Soc. Philadelphia 4: 181. Cuba.
formula Viereck, 1902. Proc. Acad. Nat. Sci. Philadelphia 54: 728. U.S. (California).
garciana Cockerell, 1907. Entomologist 40: 265. Southwestern U.S. (New Mexico, Texas).
gutierreziae Cockerell, 1896. Canadian Entomol. 28: 284. Southwestern U.S., northern Mexico.
heiligbrodti Cresson, 1878. Trans. American Entomol. Soc. 7: 75. Eastern U.S.
  tiftonensis Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 610.
  modesta rivertonensis Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 610.
hondurasica Cockerell, 1949. Proc. U.S. Natl. Mus. 98: 458. Central America (Honduras).
infrequens Smith, 1879. Descriptions of New Species of Hymenoptera in the Collection of the British Museum, p. 99. South America (Brazil).
jamaicensis Cockerell, 1912. Ann. Mag. Nat. Hist. (8)10: 484. Jamaica.
krugii Cresson, 1878. Trans. American Entomol. Soc. 7: 75. West Indies.
lamarensis Cockerell, 1905. Bull. Colorado Agr. Expt. Sta. 94: 76. Western U.S. (Colorado, Texas).
limata Cresson, 1878. Trans. American Entomol. Soc. 7: 76. Mexico, U.S. (Texas).

montezumia Smith, 1879. Descriptions of New Species of Hymenoptera in the Collection of the British Museum, p. 101. Mexico.
limata var. *xanthaspis* Cockerell, 1949. Proc. U.S. Natl. Mus. 98: 457. Honduras.
lippiae lippiae Cockerell, 1903. Ann. Mag. Nat. Hist. (7)12: 214. Southwestern U.S. (New Mexico).
lippiae sublippiae Cockerell, 1907. Southwestern U.S. (New Mexico).
lippiae var. *sublippiae* Cockerell, 1907. Entomologist 40: 265.
melanoptera Cockerell, 1921. American Mus. Novitates 24: 5. Western U.S. (Colorado).
mexicana Cresson, 1878. Trans. American Entomol. Soc. 7: 76. Mexico.
?*mimus* (Cockerell), 1916. Entomol. News 27: 209. South America (Brazil). [*Polybiapis*] (**new combination**).
mitchelli Cockerell, 1911. Proc. U.S. Natl. Mus. 39: 654. U.S. (Texas).
?*multicolor* Ducke, 1910. Rev. d'Entomol.(Caen) 28: 106. South America (Chile).
neomexicana Cockerell, 1903. Ann. Mag. Nat. Hist. (7)12: 209. Southwestern U.S. (New Mexico).
nigrescens Friese, 1921. Central America (Costa Rica).
xanthopus var. *nigrescens* Friese, 1921. Stettiner Entomol. Ztg. 82: 92.
nitidiceps Cockerell, 1931. Ann. Mag. Nat. Hist. (10) 8: 547. Southeastern Mexico (Yucatán).
pallidelutea Swenk, 1915. Univ. Stud. (Lincoln, Nebraska) 15: 186. U.S. (Arizona), Mexico (Baja California).
peninsularis Cockerell, 1925. Pan-Pac. Entomol. 1:180. ["*penisularis*" in Hurd, 1979, p. 2112, is a lapsus calami, not Cockerell's original spelling].
pampicola Holmberg, 1886. An. Soc. Cient. Argentina 22: 236. South America.
?*pampicola* var. *flavescens* Friese, 1916 (nec *fucata* var. *flavescens* Friese, 1921). Stettiner Entomol. Ztg. 77: 339. Central America (Costa Rica).
?*pampicola* var. *fuliginosa* Friese, 1916. Stettiner Entomol. Ztg. 77: 339. Bolivia.
?*pampicola* var. *sanguinolenta* Friese, 1916. Stettiner Entomol. Ztg. 77: 339. Brazil.
panamensis Michener, 1954. Bull. American Mus. Nat. Hist. 104: 118. Central America (Panama).
pilipes (Cresson), 1865. Proc. Entomol. Soc. Philadelphia 4: 183. West Indies. [*Pasites*].
?*polybioides* Ducke, 1908. Rev. d'Entomol. 27: 37. South America (Brazil).
putnami Cresson, 1876. Proc. Davenport Acad. Nat. Sci. 1: 210. West-central U.S.
ridingsii Cresson, 1878. Trans. American Entomol. Soc. 7:74. Western U.S. (Colorado).
?*rugicollis rugicollis* Friese, 1916. Stettiner Entomol. Ztg. 77: 339. South and Central America (Costa Rica, Argentina, Paraguay).
?*rugicollis ecuadoria* Friese, 1916. Stettiner Entomol. Ztg. 77: 340. South America (Ecuador).
semisuavis Cockerell, 1910. Psyche 17: 92. Western U.S. (California, Washington).
simplicicoxa Swenk, 1915. Univ. Stud. (Lincoln, Nebraska) 15: 182. Southwestern U.S. (Arizona).
suavis Cresson, 1878. Trans. American Entomol. Soc. 7: 74. Northwestern U.S. (California, Idaho, Oregon, Washington).
flavipes Provancher, 1888. Additions et Corrections au Vol. II de la Faune Entomologique du Canada, Traitant des Hyménoptères, p. 426.
?*subscopifera* Ducke, 1908. Rev. d'Entomol. 27: 36. South America.
tenuicornis Cockerell, 1949. Proc. U.S. Natl. Mus. 98: 456. Central America (Honduras).
texana Cresson, 1872. Trans. American Entomol. Soc. 4: 271. Eastern and central U.S., west to Colorado and Arizona.
tibialis Cresson, 1865. Proc. Entomol. Soc. Philadelphia 4: 182. Cuba.
cruralis Moure, 1960. Stud. Entomol. 3: 160.
?*tomentifera* Ducke, 1907. Zeitschr. Syst. Hymen. Dipt. 7: 459. South America (Brazil).
trapidoi Michener, 1954. Bull. American Mus. Nat. Hist. 104: 119. Central America (Panama).
uhleri Cockerell, 1905. Bull. Colorado Agr. Expt. Sta. 94: 77. Western U.S. (Colorado).
vegana Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 610. Eastern U.S.
modesta Cresson, 1863 (nec Herrich-Schäffer, 1839; nec Schmiedeknecht, 1882). Proc. Entomol. Soc. Philadelphia 2: 286. Preoccupied.
modesta var. *vegana* Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 610.
vegana var. *nitescens* Cockerell, 1905. Bull. Colo. Agr. Expt. Sta. 94: 76.
vierecki Cockerell, 1903. Ann. Mag. Nat. Hist. (7)12: 211. Central and southwestern U.S., northern Mexico.
vierecki convolvuli Swenk, 1913. Univ. Stud.(Lincoln, Nebraska) 12: 109.
vierecki race *cushmani* Cockerell, 1926. Ann. Mag. Nat. Hist. (9)17: 307.
wisconsinensis Graenicher, 1911. Bull. Pub. Mus. Milwaukee 1: 239. North-central U.S. (Wisconsin).
xanthopus Friese, 1921. Stettiner Entomol. Ztg. 82: 91. Central America (Costa Rica).
zamoranica Cockerell, 1949. Proc. U.S. Natl. Mus. 98: 458. Central America (Honduras).

roberjeotiana group
(paraphyletic)

Nomadita Mocsáry, 1894. Termes. Fuzetek 17: 37. Type species: *Nomadita montana* Mocsáry, 1894; monobasic.
Nomada subgenus *Gallinomada* Rodeck, 1945. Entomol. News 56: 181. Type species: *Nomada antonita* Cockerell, 1909; original designation.

Names preceded by a question mark in the list below represent species that are inferred to belong to this group on the basis of the original descriptions. Most of these are Japanese species described from unique specimens by Tsuneki, whose descriptions are very detailed. The Afrotropical species *cordillera* is known only from the female, and is placed here on the basis of Eardley and Schwarz's (1991) judgment that it is closely related to species such as *africana*, *guichardiana*, and *hararensis*, which clearly do belong in the *roberjeotiana* group. The Afrotropical species *aethiopica* and *aurantifascia*, also known only from the female, cannot confidently be placed in this group. As discussed in Alexander (1994), the recently discovered male of *N. whiteheadi* from the Cape Province of South Africa has terminalia that suggest an affinity with the *roberjeotiana* group. Two "varieties" of *errans* described by Friese are also preceded by a question mark because we have not seen the specimens upon which the names are based, and Friese's varietal names are often questionable.

abyssinica Meade-Waldo, 1913. Ann. Mag. Nat. Hist (8)12: 101. East Africa (Ethiopia).
africana Friese, 1911. Zool. Jahrb. Abt. Syst. Geogr. Biol. Tiere 30: 675. Equatorial Africa (Nigeria, Ethiopia).
?*albidemaculata* Lozinski, 1922. Bull. Int. Acad. Polonaise Sci. Let. Cl. Sci. Math. Nat. Ser. B : 104. Eastern Siberia.
aquilarum Cockerell, 1903. Ann. Mag. Nat. Hist. (7)12: 208. North-central U.S., western and central Canada.
cockerelli Graenicher, 1911. Bull. Pub. Mus. Milwaukee 1: 240.
dacotensis Swenk, 1913. Univ. Stud. (Lincoln, Nebraska) 12: 88.
arasiana Tsuneki, 1973. Etizenia 66(1): 44. Japan (Honshu).
?*buyoo* Tsuneki, 1976. Kontyu 44: 49. Japan (Hokkaido).

cleopatra Schwarz, 1989. Linzer Biol. Beitr. 21: 308. North Africa (Egypt, Morocco), Iran.
?*cordillera* Eardley & Schwarz, 1991. Phytophylactica 23: 26. Ethiopia.
ecarinata Morawitz, 1888. Hor. Soc. Entomol. Ross. 22: 257.Russia (Siberia).
elegantula Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 578. Western U.S. (California, Idaho).
errans Lepeletier, 1841. Histoire Naturelle des Insectes, Hyménoptères, v. 2, p. 473. Southern and central Europe.
errans var. *korleviciana* Friese, 1921. Deutsche Entomol. Zeitschr. 1921: 254. Croatia.
errans var. *sibirica* Friese, 1921. Deutsche Entomol. Zeitschr. 1921: 255. Siberia.
transsylvanica Endre, 1927. Ver. Siebenbuerg. Ver. Naturw. 77: 19.
?*esana* Tsuneki, 1973. Etizenia 66(1): 36. Japan (Hokkaido).
?*etigonis* Tsuneki, 1986. Spec. Publ. Japan Hymen. Assoc. 32: 57. Japan (Honshu).
eximia Eardley & Schwarz, 1991. Phytophylactica 23: 26. South Africa (Transvaal).
galloisi Yasumatsu & Hirashima, 1953. Kontyu 20: 34. Japan (Honshu, Hokkaido).
guichardiana Eardley & Schwarz, 1991. Phytophylactica 23: 22. Ethiopia.
hakusana hakusana Tsuneki, 1973. Etizenia 66(1): 32. Japan (Honshu, Hokkaido), **new combination**.
melanura hakusana Tsuneki, 1973. Etizenia 66(1): 32. (*Nomada melanura* Tsuneki is preoccupied).
momoglonis hakusana Tsuneki, 1975. Kontyu 43: 463. (Incorrectly proposed as new name for *melanura hakusana* Tsuneki).
hakusana momoglonis Tsuneki, 1975. Kontyu 43: 463. **new combination**.
melanura melanura Tsuneki, 1973 (nec Mocsáry 1883). Etizenia 66(1): 30. Japan (Honshu, Hokkaido). Preoccupied.
momoglonis momoglonis Tsuneki, 1975. Kontyu 43: 463. (Incorrectly proposed as new name for *melanura melanura* Tsuneki 1973).
hararensis Meade-Waldo, 1913. Ann. Mag. Nat. Hist. (8)12: 102. Ethiopia.
issikii Yasumatsu, 1939. Trans. Kansai Entomol. Soc. 9: 5. Japan (Hokkaido, Honshu).
koikensis Tsuneki, 1973. Etizenia 66(1): 46. Japan (Honshu).
kusdasi Schwarz, 1981. Entomofauna 2: 380. Turkey, Israel.
?*marginella* Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 576. Western U.S. (California).
mckenziei Timberlake & Cockerell, 1937. American Mus. Novitates 948: 4. Western U.S. (California).
melanosoma Cockerell, 1916. Pomona Coll. Jour. Entomol. Zool. 8: 55. Western U.S. (California).
munakatai Tsuneki, 1973. Etizenia 66(1): 39. Japan (Hokkaido).
mutans Cockerell, 1910. Psyche 17: 91. Northwestern U.S.
obtusifrons Nylander, 1848. Notis. Sällsk. Fauna Fl. Fennica Förh. 1: 184. Throughout Europe.
mistura Smith, 1851. Zoologist 9, App. p. CXXVII.
robertjeotana var. *alpina* Morawitz, 1867. Hor. Soc. Entomol. Ross. 5: 69.
okamotonis okamotonis Matsumura, 1912. Thousand Insects of Japan, Suppl. 4: 198. Japan (Hokkaido), Northeast Asia.
okamotonis kaiensis Tsuneki, 1976. Kontyu 44: 157. Japan (Honshu).
palmeni Morawitz, 1888. Hor. Soc. Entomol. Ross. 22: 253. Russia (western Siberia).
placida Cresson, 1863. Proc. Entomol. Soc. Philadelphia 2: 291. Northeastern and central U.S., Canada (Ontario).
roberjeotiana roberjeotiana Panzer, 1799. Fauna Insectorum Germanicae (72): 18. Eurasia.
montana (Mocsáry), 1894 (nec Scopoli, 1763). Termes. Fuzetek. 17: 37 [*Nomadita*].
neglecta Herrich-Schäffer, 1839. Zeitschr. Entomol. 1: 283.
panzeriana Walckenaer, 1802. Faune Parisienne 2: 114.
roberjeotiana tormentillae Alfken, 1901. Zeitschr. Syst. Hymen. Dipt. 1: 221.
roberjeotiana aino Tsuneki, 1973. Japan (Hokkaido).
aino Tsuneki, 1973. Etizenia 66(1): 40.
rufipes Fabricius, 1793 (nec Schenck, 1870). Entomologia Systematica 2: 347. Throughout Europe.
fennica Alfken, 1924. Notul. Entomol. 4: 36.
picta (Kirby) 1802. Monographia Apum Angliae, v. 2, p. 206 [*Apis*].
rufopicta (Kirby) 1802. Monographia Apum Angliae, v. 2, p. 207 [*Apis*].
solidaginis Panzer, 1799. Fauna Insectorum Germanicae (72): 18.
rufipes nigriventris Alfken, 1926. Verh. Ver. Naturw. Unterh. Hamburg 18: 49.
solidaginis var. *punctulifera* Friese, 1921. Deutsche Entomol. Zeitschr. 1921: 252.
solidaginis var. *minutula* Friese, 1921. Deutsche Entomol. Zeitschr. 1921: 253.
vaga Panzer, 1798. Fauna Insectorum Germanicae, Heft 55, p. 22.
sempiterna Morawitz, 1894. Hor. Soc. Entomol. Ross. 29: 58. southwest Asia (Turkestan).
snowii Cresson, 1878. Trans. American Entomol. Soc. 7: 75. North-central U.S., Colorado.
antonita Cockerell, 1909. Canadian Entomol. 41: 35.
omahaensis Swenk, 1915. Univ. Stud. (Lincoln, Nebraska) 15: 171.
spinicoxa Schwarz, 1987. Entomofauna 8: 468. Tadzhikistan.
?*temmasana* Tsuneki, 1986. Spec. Publ. Japan Hymen. Assoc. 32: 34. South Korea.
?*tiendang* Tsuneki, 1986. Spec. Publ. Japan Hymen. Assoc. 32: 32. North China.
timberlakei Broemeling, 1988. Pan-Pac. Entomol. 64: 333.Western U.S. (California).
verecunda Cresson, 1879. Trans. American Entomol. Soc. 7: 203. Western U.S. (California, Nevada, Oregon).
waltoni Cockerell, 1910. Entomologist 43: 239. Tibet.
?*whiteheadi* Eardley & Schwarz, 1991. Phytophylactica 23: 18. South Africa .
xanthophila Cockerell, 1900. Ann. Mag. Nat. Hist. (7)5: 414. Southwestern U.S. (New Mexico).
?*yanoi* Tsuneki, 1973. Etizenia 66(1): 37. Japan (Kyushu, south Honshu).

erigeronis group

Centrias Robertson, 1903. Canadian Entomol. 35: 174, 176. Type species: *Nomada erigeronis* Robertson, 1897; original designation.
Nomada subgenus *Nomadula* Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 611. Type species: *Nomada articulata* F. Smith, 1854; original designation.

articulata Smith, 1854. Catalogue of the Hymenoptera in the Collection of the British Museum, v.2, p. 248. Central and eastern U.S.
?*americana* Kirby, 1837. Fauna Boreali Americana 4: 269. (type missing, species uncertain).
americana dacotana Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 592
bilobata Swenk, 1913. Univ. Stud. (Lincoln, Nebraska) 12: 25. female, not male.
incerta Cresson, 1863. Proc. Entomol. Soc. Philadelphia 2: 309.
australis Mitchell, 1962. North Carolina Agr. Expt. Sta. Tech. Bull. 152: 367. Southeastern U.S., north to New York and Indiana.
?*corvallisensis* Cockerell, 1903. Ann. Mag. Nat. Hist. (7)12: 207. Northwestern U.S. (Oregon).
crotchii crotchii Cresson, 1878. Trans. American Entomol. Soc. 7: 81. Western U.S. (California).

crotchii nigrior Cockerell, 1903. Western U.S. (California).
crotchii var. *nigrior* Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 564.
erigeronis Robertson, 1897. Trans. Acad. Sci. St. Louis 7: 341. Central and northeastern U.S.
erigerontis Robertson, 1928. Flowers and Insects, Carlinville, Illinois, pp. 9, 66, 69.
erythrochroa Cockerell, 1903. Ann. Mag. Nat. Hist. (7)12: 203. Northwestern U.S. (Washington, Idaho)
erythrospila Cockerell, 1916. Pomona Coll. Jour. Entomol. Zool. 8: 56. Western U.S. (California).
frieseana Cockerell, 1904. Ann. Mag. Nat. Hist. (7)14: 28. Western U.S. (Colorado).
?*malonina* Cockerell, 1910. Psyche 17: 94. Northwestern U.S. (Washington).
martinella Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 590. Western U.S. (New Mexico, Colorado).
melliventris Cresson, 1878. Trans. American Entomol. Soc. 7: 82. Western U.S. (California).
pascoensis Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 564. Western U.S. (California, Washington).
rohweri aureopilosa Swenk, 1913. Western U.S. (Colorado).
aureopilosa Swenk, 1913. Univ. Stud. (Lincoln, Nebraska) 12: 111.
rohweri rohweri Cockerell, 1906. Bull. American Mus. Nat. Hist. 22: 438. Western U.S. (Colorado).
rubicunda Olivier, 1811. Encyclopédie Méthodique. Dictionnaire des Insectes, v. 8, p. 365. Central and eastern U.S.
torrida Smith, 1854. Catalogue of the Hymenoptera in the Collection of the British Museum, v.2, p. 250.
scita Cresson, 1878. Trans. American Entomol. Soc. 7: 77. West-central U.S. (Colorado, Nebraska, North Dakota).
scitiformis Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 591. Western U.S. (Oregon).
semiscita Cockerell, 1904. Ann. Mag. Nat. Hist. (7)14: 29. Western U.S. (Colorado).
seneciophila Mitchell, 1962. North Carolina Agr. Expt. Sta. Tech. Bull. 152: 370. Southeastern U.S. (North Carolina, Florida).
sophiarum Cockerell, 1903. Ann. Mag. Nat. Hist. (7)12: 213. Southwestern U.S. (New Mexico).

Nomada rodecki

This problematic species is known only from a single male specimen in the collection of the National Museum of Natural History, Washington, D.C. (holotype No. 75223). Its uncertain phylogenetic placement is discussed in Alexander (1994).

rodecki Mitchell, 1962. North Carolina Agr. Expt. Sta., Tech. Bull. No. 152, p. 376. Eastern U.S. (North Carolina).

ruficornis group
(paraphyletic?)

Nomada Scopoli, 1770. Annus Historico Naturalis, 4. p. 44. Type species: *Apis ruficornis* Linnaeus, 1758; designated by Curtis (1832).
Gnathias Robertson, 1903. Canadian Entomol. 35: 173, 175-176. Type species: *Nomada bella* Cresson, 1863; original designation.
Nomada subgenus *Heminomada* Cockerell & Atkins, 1902. Ann. Mag. Nat. Hist. (7)10: 42. Type species: *Nomada obliterata* Cresson, 1863; original designation.
Lamproapis Cameron, 1902. Jour. Bombay Nat. Hist. Soc. 14: 419-420. Type species: *Lamproapis maculipennis* Cameron, 1902; monobasic.
Phor Robertson, 1903. Canadian Entomol. 35: 174. Type species: *Nomada integerrima* Dalla Torre, 1896 (= *Nomada integra* Robertson, 1893; preoccupied); original designation and monobasic.
Xanthidium Robertson, 1903. Canadian Entomol. 35: 174, 177. Type species: *Nomada luteola* Olivier, 1811; original designation.
Includes *zonata* group of Stöckhert, 1941. Mitt. Münchner Entomol. Ges. 31: 1072-1122.

The list presented here indicates synonyms as they are currently established in *published* work. Our primary objective is to assemble the names in one place so that they will be more accessible to future workers dealing with species-level taxonomy, and not to present this as a definitive treatment of the species names for this group. North American and Japanese species currently known only from females are preceded by an asterisk, to emphasize that their placement in this group is provisional until the males are known. (There are a few exceptional cases in which females exhibit striking apomorphies that enable them to be associated with species in which males are known.) Species names preceded by a question mark are those for which we have seen no accurately determined specimens.

?*abtana* Tsuneki, 1973. Etizenia 66(2): 126. Japan (Hokkaido).
accepta Cresson, 1878. Trans. American Entomol. Soc. 7: 77. West-central U.S. (Kansas, Colorado).
pacata Cresson, 1878. Trans. American Entomol. Soc. 7: 81.
**acutilabris* Schwarz, 1990. Entomofauna, Supplement 5: 25. Northwestern India.
agynia Cockerell, 1905. Bull. Colorado Agr. Expt. Sta. 94: 81. Western U.S. (Colorado).
alboguttata alboguttata Herrich-Schäffer, 1839. Zeitschr. Entomol. 1: 282. Widespread in Palearctic.
alboguttata var. *liburnica* Friese, 1921. Deutsche Entomol. Zeitschr. 1920: 252.
alboguttata var. *suerinensis* Friese, 1921. Deutsche Entomol. Zeitschr. 1920: 252.
ochrostoma Zetterstedt, 1838 (nec Kirby, 1802). Insecta Lapponica Descripta, v. 1, p. 470.
quinquespinosa Thomson, 1870. Opuscula Entomologica 2: 93.
alboguttata etizenensis Tsuneki, 1975. Kontyu 43: 467. Japan (Honshu).
**alboscutellata* Schwarz, 1990. Entomofauna, Supplement 5: 16. India.
aldrichi Cockerell, 1910. Northwestern N. America.
vicinalis aldrichi Cockerell, 1910. Ann. Mag. Nat. Hist. (8)5: 368.
algira Mocsáry, 1883. Magy. Akad. Természz. Értek. 13: 60. Algeria, southern France(?).
platyzona Pérez, 1884. Act. Soc. Linn. Bordeaux 37: 343.
**alpha alpha* Cockerell, 1905. Western U.S. (Colorado).
alpha Cockerell, 1905. Bull. Colorado Agr. Expt. Sta. 94: 84.
**alpha dialpha* Cockerell, 1921. Western U.S. (Colorado).
**alpha* var. *dialpha* Cockerell, 1921. American Mus. Novitates 24: 3.
**alpha paralpha* Cockerell, 1921. Western U.S. (Colorado).
**alpha* var. *paralpha* Cockerell, 1921. American Mus. Novitates 24: 3.
amabilis Radoszkowski, 1876. Hor. Soc. Entomol. Ross. 12: 94. Southwest Asia (Caucasus).
?*amamiensis* Hirashima, 1960. Mushi 33: 60. Japan, Korea.
?*amoena* Cresson, 1863. Proc. Entomol. Soc. Philadelphia 2: 300. North-central U.S. (Illinois) [type lost].
amurensis Radoszkowski, 1876. Hor. Soc. Entomol. Ross. 12: 91. Eastern Siberia.
anatolica Pittioni, 1952. Ann. Naturh. Mus. Wien 59: 245. Nomen novum for *inermis* Friese, 1921 (nec Pérez, 1895). Syria, Asia Minor, Caspian Sea region.
inermis Friese, 1921. Deutsche Entomol. Zeitschr. 1920: 259.
**angelarum* Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 574. Western U.S. (California).
**angulata* Swenk, 1913. Univ. Stud. (Lincoln, Nebraska) 12: 40. West-central U.S. (Nebraska).
annexa Nurse, 1904. Jour. Bombay Nat. Hist. Soc. 15: 572. India.
**annulata* Smith, 1854. Catalogue of the Hymenoptera in the Collection of the British Museum, v.2, p. 248. Southeastern U.S.

aprilina Swenk, 1913. Univ. Stud. (Lincoln, Nebraska) 12: 28. Central U.S. (Nebraska).

**ariasi* Dusmet, 1913. Mem. R. Soc. Española. Hist. Nat. 9: 258. Spain.

pastoralis Schmiedeknecht, 1882 (nec Eversmann, 1852). Apidae Europaeae 1: 118. Preoccupied.

gracillima Lozinski, 1922. Bull. Int. Acad. Polonaise Sci. Let. Cl. Sci. Math. Nat. Ser. B 1921: 110. Nomen novum for *pastoralis* Schmiedeknecht).

arida Nurse, 1903. Ann. Mag. Nat. Hist. (7)11: 544. Northern India (Kashmir).

arizonica Cockerell, 1911. Proc. U.S. Natl. Mus. 41: 242. Southwestern U.S. (Arizona).

armatella Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 606. Northeastern and northcentral U.S., west to Michigan.

arrogans Schmiedeknecht, 1882. Apidae Europaeae 1: 95. Greece.

ashabadensis Schwarz, 1987. Entomofauna 8: 453. Southwest Asia (Turkmenistan, Tadzhikistan).

**ashmeadi* Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 568. Western U.S. (California).

?**asozuana* Tsuneki, 1975. Kontyu 43: 475. Japan (Honshu).

**astori* Cockerell, 1903. Ann. Mag. Nat. Hist. (7)12: 206. Northwestern U.S. (Oregon).

aswensis Tsuneki, 1973. Etizenia 66 (2): 100. Japan (Honshu).

**atrofrontata* Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 573. Western U.S. (southern California).

?*atrohirta* Friese, 1923. *In:* Friese and von Schulthess, 1923. Konowia 2: 279. North Africa.

atroscutellaris Strand, 1921. Eastern and southern Europe.

furva var. *atroscutellaris* Strand, 1921. Arch. Naturg. 87A Heft 3: 300.

**augustiana* Mitchell, 1962. North Carolina Agr. Expt. Sta. Tech. Bull. 152: 402. Southeastern U.S. (Georgia).

autumnalis Mitchell, 1962. North Carolina Agr. Expt. Sta. Tech. Bull. 152: 382. Northcentral U.S. (Michigan).

**avalonica* Cockerell, 1938. Ann. Mag. Nat. Hist. (11)2: 152. Western U.S. (California).

azaleae Mitchell, 1962. North Carolina Agr. Expt. Sta. Tech. Bull. 152: 403. Southeastern U.S. (North Carolina).

baccata baccata Smith, 1844. Zoologist 2: 409. Northern and central Europe.

laeta Thomson, 1870. Opuscula Entomologica, v. 2, p. 93.

baccata hrubanti Balthasar, 1958. Acta Soc. Entomol. Cechoslovenicae 55: 344. Eastern Europe (Hungary).

banksi Cockerell, 1907. Entomologist 40: 98. Eastern North America.

barbilabris Pérez, 1895. Espèces Nouvelles de Mellifères de Barbarie, p. 29. Northwest Africa.

cabrerai Dusmet, 1915. Mem. R. Soc. Española Hist. Nat. 8 (Mem. 7): 313.

dido Pérez, 1895. Espèces Nouvelles de Mellifères de Barbarie, p. 31.

barcelonensis barcelonensis Cockerell, 1917. Ann. Mag. Nat. Hist. (8)20: 237. Nomen novum for *excellens* Pérez, 1913 (nec Cockerell, 1903). Spain.

excellens Pérez, 1913. Bol. R. Soc. Española Hist. Nat. 13: 323. Preoccupied.

barcelonensis montarcosi Dusmet, 1935. Spain.

excellens montarcosi Dusmet, 1935. Mem. Soc. Entomol. Española, Zaragosa, No. 4a.

beata Nurse, 1903. Ann. Mag. Nat. Hist. 8(11): 543. India (Kashmir).

bella bella Cresson, 1863. Proc. Entomol. Soc. Philadelphia 2: 287. Eastern North America.

albofasciata Smith, 1879. Descriptions of New Species of Hymenoptera in the Collection of the British Museum, p. 100.

bella callura Cockerell, 1911. Proc. U.S. Natl. Mus. 39: 657. Western U.S. (Colorado).

bethunei Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 607. North-central U.S. (Michigan, Ohio).

**beulahensis* Cockerell, 1903. Ann. Mag. Nat. Hist. (7)12: 209. U.S. (New Mexico, North Dakota).

bicrista Swenk, 1913. Univ. Stud. (Lincoln, Nebraska) 12: 27. Central U.S. (Nebraska).

bifurcata Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 577. Western U.S. (California).

bisetosa Swenk, 1913. Univ. Stud. (Lincoln, Nebraska) 12: 30. Central U.S. (Nebraska).

bishoppi Cockerell, 1911. Eastern and central U.S.

luteola bishoppi Cockerell, 1911. Proc. U.S. Nat. Mus. 39: 655.

bisignata Say, 1824. *In* Keating, Narrative of an expedition...under the command of Major Long, v. 2, (App.), p. 354. "United States".

bicincta Howard, 1902. Insect Book, pl.3, fig. 32. Lapsus calami?

?*bolivari* Dusmet, 1913. Mem. R. Soc. Española Hist. Nat. 9: 379. Spain.

braunsiana braunsiana Schmiedeknecht, 1882. Southern Europe.

braunsiana Schmiedeknecht, 1882. Apidae Europaeae 1: 144.

braunsiana umbrosa Schmiedeknecht, 1882. Greece.

braunsiana var. *umbrosa* Schmiedeknecht, 1882. Apidae Europaeae 1: 144.

**californiae* Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 571. Western U.S. (California).

calimorpha Schmiedeknecht, 1882. Apidae Europaeae 1: 33. Southern Europe and western Asia.

copetica Morawitz, 1895. Hor. Soc. Entomol. Ross. 29: 49.

calloptera Cockerell, 1918. Ann. Mag. Nat. Hist. (9)2: 479. Japan (Honshu).

calloxantha Cockerell, 1921. American Mus. Novitates 24: 4. Western U.S. (Wyoming).

capillata Mitchell, 1962. North Carolina Agr. Expt. Sta. Tech. Bull. 152: 406. Eastern U.S. (Massachusetts).

capitalis Mitchell, 1962. North Carolina Agr. Expt. Sta. Tech. Bull. 152: 385. Eastern U.S.

carinicauda Cockerell, 1921. American Mus. Novitates 24: 7. Western U.S. (Colorado).

castellana Dusmet, 1913. Mem. R. Soc. Española Hist. Nat. 9: 309. Spain, Tirol, central Germany.

baeri Stöckhert, 1930. *In* Schmiedeknecht. Die Hymenopteren Nord- und Mitteleuropas, pp. 1008, 1044.

ceanothi Cockerell, 1907. Entomologist 40: 97. Eastern U.S. (New York to North Carolina).

centenarii Dusmet, 1932. Eos 8: 233. Northwest Africa.

chrysopyga chrysopyga Morawitz, 1872. Hor. Soc. Entomol. Ross. 8: 288. Southern Europe, Asia Minor, North Africa.

sericultorum Schulz, 1906. Spolia Hymenopterologica, p. 259. Nomen novum for *superba* Pérez, 1902 (nec Cresson, 1863).

speciosissima Schmiedeknecht, 1882. Apidae Europaeae 1: 103.

superba Pérez, 1902. Proc.-Verb. Soc. Linn. Bordeaux 57: lx. Preoccupied.

syriaca Friese, 1921. Deutsche Entomol. Zeitschr. 1920: 261.

chrysopyga pyrosoma Dours, 1873. North Africa.

mamillaris Pérez, 1895. Espèces Nouvelles de Mellifères de Barbarie, p. 29.

nigrita Pérez, 1895 (nec Schenck, 1859). Espèces Nouvelles de Mellifères de Barbarie, p. 29.

chrysopyga var. *pharaonis* Friese, 1921. Deutsche Entomol. Zeitschr. 1920: 256.

pyrosoma Dours, 1873. Rev. Mag. Zool. (3)1: 308.

rubrolineata Pittioni, 1952. Ann. Naturh. Mus. Wien 59: 287. Nomen novum for *nigrita* Pérez, 1895 (nec Schenck, 1859).

scutellata Saunders, 1908 (nec Friese, 1920). Trans. Entomol. Soc. London 2: 228.

chrysopyga form *umbripennis* Alfken, 1924. Deutsche Entomol. Zeitschr. 1924: 247.

**citrina citrina* Cresson, 1878. Trans. American Entomol. Soc. 7: 79. Pacific coast of North America.
citrina flavomarginata Swenk, 1913. Univ. Stud. (Lincoln, Nebraska) 12: 67. Central U.S. (Nebraska).
**citrina rufula* Cockerell, 1903. Northwestern U.S. (Idaho).
citrina var. *rufula* Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 586.
civilis civilis Cresson, 1878. Trans. American Entomol. Soc. 7: 78. U.S. west of Nebraska.
**civilis spokanensis* Cockerell, 1910. Psyche 17: 92. Western U.S. (Washington).
**clarescens* Cockerell, 1921. American Mus. Novitates 24: 10. Western U.S. (Colorado).
**clarkii* Cockerell, 1903. Ann. Mag. Nat. Hist. (7)12: 203. Northwestern U.S. (Oregon).
**collinsiana* Cockerell, 1905. Bull. Colorado Agr. Expt. Sta. 94: 79. Western U.S. (Colorado).
coloradella Cockerell, 1905. Bull. Colorado Agr. Expt. Sta. 94: 83. Western U.S. (Colorado).
**coloradensis* Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 603. Western U.S. (Colorado).
**colorata* Mitchell, 1962. North Carolina Agr. Expt. Sta., Tech. Bull. 152: 386. Northern U.S. (New York, Michigan).
**composita* Mitchell, 1962. North Carolina Agr. Expt. Sta., Tech. Bull. 152: 408. Northern U.S. (Connecticut, Michigan).
**concinnula* Cockerell, 1921. American Mus. Novitates 24: 6. Western U.S. (Colorado).
concolor Schmiedeknecht, 1882. Apidae Europaeae 1: 201. Sicily, southern France.
quadridens Pérez, 1884. Act. Soc. Linn. Bordeaux 37: 358.
confinis Schmiedeknecht, 1882. Apidae Europaeae 1: 90. Southern Europe.
carniolica Schmiedeknecht, 1882. Apidae Europaeae 1: 196.
conjungens Herrich-Schäffer, 1839. Zeitschr. Entomol. 1: 279. Southern and central Europe, England, northwest Africa.
bipunctis Pérez, 1902. Proc.-Verb. Soc. Linn. Bordeaux 57: lxi.
dallatorreana Schmiedeknecht, 1882. Apidae Europaeae 1: 194.
?consobrina Dufour, 1841. Mém. Mat. Savants Étrangers 7: 422. Europe (France).
coquilletti Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 567. Northwestern U.S. (California, Idaho, Washington).
cordleyi Cockerell, 1903. Ann. Mag. Nat. Hist. (7)12: 445. Northwestern U.S. (Oregon).
coxalis coxalis Morawitz, 1877. Hor. Soc. Entomol. Ross. 14: 107. (Iran, Pakistan, Caucasus, Turkey, Israel).
coxalis cretensis Schulz, 1906. Spolia Hymenopterologica, p. 67. Crete.
crawfordi crawfordi Cockerell, 1905. Bull. Colorado Agr. Expt. Sta. 94: 79. West-central U.S. (Colorado, Nebraska, Wyoming).
**crawfordi lachrymosa* Cockerell, 1921. American Mus. Novitates 24: 5. Western U.S. (Wyoming).
cressonii cressonii Robertson, 1893. Trans. American Entomol. Soc. 20: 275. Eastern and central U.S.
mera Cockerell, 1908. Proc. Entomol. Soc. Washington 10: 83.
cressonii trevoriana Cockerell, 1905. Canadian Entomol. 37: 285. Northwestern U.S. (Washington).
**crudelis* Cresson, 1878. Trans. American Entomol. Soc. 7: 82. Southeastern U.S. (Georgia).
cruenta cruenta Schmiedeknecht, 1882. Apidae Europaeae 1: 170. Eastern Europe, Greece, Sicily.
cruenta sexspinosa Friese, 1921. Turkey.
chrysopyga var. *rubescens* Lozinski, 1922. Bull. Int. Acad. Polonaise Sci. Let. Cl. Sci. Math. Nat. Ser. B 1921: 109.
sexspinosa Friese, 1921. Deutsche Entomol. Zeitschr. 1920: 260.
cuneata (Robertson), 1903. Canadian Entomol. 35: 175 [*Gnathias*]. Eastern North America.
Gnathias cuneatus form *decemnotatus* Robertson, 1903. Canadian Entomol. 35: 175.
Gnathias cuneatus form *octonotatus* Robertson, 1903. Canadian Entomol. 35: 175.
Gnathias cuneatus form *quadrisignatus* Robertson, 1903. Canadian Entomol. 35: 176.
Gnathias cuneatus form *sexnotatus* Robertson, 1903. Canadian Entomol. 35: 176.
custeriana Cockerell, 1911. Proc. U.S. Natl. Mus. 41: 241. Western U.S. (Colorado).
**cymbalariae* Cockerell, 1906. Bull. American Mus. Nat. Hist. 22: 439. Western U.S. (Colorado).
**davidsoni* Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 575. Western U.S. (California).
debilis Timberlake, 1954. Pan-Pac. Entomol. 30: 135. Western U.S. (California).
decempunctata Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 565. Western U.S. (California).
**decepta* Mitchell, 1962. North Carolina Agr. Expt. Sta. Tech. Bull. 152: 411. Northern and central U.S.
dentariae (Robertson), 1903. Canadian Entomol. 35: 178. Eastern and central U.S. [*Xanthidium*].
denticulata Robertson, 1902. Canadian Entomol. 34: 49. Central and eastern U.S.
simplex Robertson, 1902. Entomol. News 13: 80.
**depressa* Cresson, 1863. Proc. Entomol. Soc. Philadelphia 2: 302. Central and eastern U.S.
depressicauda Cockerell, 1908. Entomol. News 19: 323.
detecta Nurse, 1904. Jour. Bombay Nat. Hist. Soc. 15: 571. Pakistan (Quetta).
detrita Mitchell, 1962. North Carolina Agr. Expt. Sta. Tech. Bull. 152: 414. Northeastern U.S. (New Hampshire).
?diervillae Tsuneki, 1973. Etizenia 66 (2): 138-139. Japan (north Honshu).
**dilucida* Cresson, 1878. Trans. American Entomol. Soc. 7: 80. Western U.S. (Colorado).
dira Schmiedeknecht, 1882. Apidae Europaeae 1: 153. Southern Europe, North Africa.
praestans Saunders, 1908. Trans. Entomol. Soc. London 2: 230.
sagana Mocsáry, 1883. Magy. Akad. Termész. Értek. 13: 61.
vergiliana Pérez, 1913. Bol. R. Soc. Española Hist. Nat.. 13: 330.
**discicollis* Morawitz, 1875. Izv. Imp. Obshch. Ljubrit. Estest. Antrop. Etnogr. 19(2): 153. Southwest Asia (Turkestan).
discrepans Schmiedeknecht, 1882. Apidae Europaeae 1: 119. Southern Europe, north to Switzerland, Hungary.
?dives Erichson, 1849. Mem. Acad. Imp. Sci. St. Petersbourg Nat. Sci. (6)7: 305. Russia (Siberia).
dreisbachi Mitchell, 1962. North Carolina Agr. Expt. Sta. Tech. Bull. 152: 414. Northcentral, northeastern U.S.
dybovskij Radoszkovsky, 1876. Hor. Soc. Entomol. Ross. 12: 93. Russia (Siberia, near Lake Baikal).
ednae Cockerell, 1907. Ann. Mag. Nat. Hist. (7)19: 537. Western U.S. (Colorado).
electa Cresson, 1863. Proc. Entomol. Soc. Philadelphia 2: 290. Eastern U.S.
mimula Cockerell, 1908. Proc. Entomol. Soc. Washington 10: 66.
**electella* Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 612. Eastern U.S. (Rhode Island to Georgia).
elrodi Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 583. Western U.S. (Montana, Nebraska, Colorado, Texas).
emarginata Morawitz, 1877. Hor. Soc. Entomol. Ross. 14: 108. Southwest Asia (Caucasus), Central and eastern Europe.
**erythraea* Dalla Torre, 1896. Catalogus Hymenopterorum, v. 10, p. 343. Nomen novum for *rubra* Provancher, 1888 (nec Geoffrey, 1785; nec Smith, 1849; nec Eversmann, 1852). Western U.S. (California).
rubra Provancher, 1888. Additions et Corrections au Vol. II de la Faune Entomologique du Canada, Traitant des Hyménoptères, p. 427 Preoccupied.
esakii Yasumatsu & Hirashima, 1953. Kontyu 20: 31. Japan (Hokkaido, Honshu, Kyushu).
fabriciana (Linnaeus), 1767 (nec Schenck, 1859). Systema Naturae, ed. 12, tomus 1, p. 955. Throughout Europe [*Apis*].

fabriciana var. *aestivalis* Friese, 1921. Deutsche Entomol. Zeitschr. 1920: 255.
nigrita Schenck, 1859 (nec Pérez, 1895). Jahrb. Ver. Naturk. Nassau 14: 194.
fabriciella (Kirby), 1802. Monographia Apum Angliae, v. 2, p. 213 [*Apis*].
germanica Panzer, 1799. Fauna Insectorum Germanicae (72): 17.
nigricornis Olivier, 1811. Encyclopédie Méthodique. Dictionnaire des Insectes, v. 8, p. 372.
quadrinotata (Kirby), 1802. Monographia Apum Angliae, v. 2, p. 214 [*Apis*].
fabriciana var. *ruficrus* Stöckhert, 1930. *In* Schmiedeknecht. Die Hymenopteren Nord- und Mitteleuropas, p. 1005.
?*fedtschenkoi* Morawitz, 1875. Izv. Imp. Obshch. Ljubrit. Estest. Antrop. Etnogr. 19(2): 149. Southwest Asia (Uzbekistan, Kazakhstan: Peski Kyzyl Kum).
fenestrata fenestrata Lepeletier, 1841. Histoire Naturelle des Insectes, Hyménoptères, v. 2, p. 476. Northern Africa, southern Europe east to Afghanistan.
affinis Dusmet, 1932 (nec Herrich-Schäffer, 1839). Eos 8: 226.
ceballosi Dusmet, 1915. Mem. R. Soc. Española Hist. Nat. 8 (Mem. 7): 325.
faventiana Pérez, 1902. Proc.-Verb. Soc. Linn. Bordeaux 57: lix.
vicarioi Dusmet, 1915. Mem. R. Soc. Española Hist. Nat. 8 (Mem. 7): 311.
fenestrata rufopleurae Schwarz, 1964. Southwest Asia (Iraq).
rufopleurae Schwarz, 1964. Polskie Pismo Entomol. 34: 59.
ferruginata (Linnaeus), 1767. Systema Naturae, ed. 12a, tomus 1, p. 958. Northern and central Europe [*Apis*].
bridgmaniana Smith, 1876. Catalogue of the British Hymenoptera in the Collection of the British Museum, p. 115.
lateralis Panzer, 1804. Systematische Nomenclatur, p. 67.
lateralis var. *blancoburgensis* Schmiedeknecht, 1882. Apidae Europaeae 1: 155.
lateralis var. *megapolitana* Schmiedeknecht, 1882. Apidae Europaeae 1: 155.
?*montana* (Scopoli), 1763 (nec Mocsáry, 1894). Entomologia Carniolica [*Apis*]. Nomen dubium.
xanthosticta (Kirby), 1802. Monographia Apum Angliae, v. 2, p. 212 [*Apis*].
fervens Smith, 1873. Trans. Entomol. Soc. London 2: 203. Japan.
**festiva* Cresson, 1863 (nec Schmiedeknecht, 1882). Proc. Ent. Soc. Philadelphia 2: 289. Northeastern U.S.
?**flammigera* Cockerell, 1906. Ann. Mag. Nat. Hist. (7)18: 71. Northwestern U.S. (Washington).
flava Panzer, 1798. Fauna Insectorum Germanicae, Heft 53, p. 21. Northern and central Europe.
?*hirsuta* Verhoeff, 1890. Entomol. Nachr. 16: 326.
intermedia Imhoff, 1834. Isis 1834: 375.
proteus Lepeletier, 1841. Histoire Naturelle des Insectes, Hyménoptères v. 2, p. 500
?*vespiformis* (Scopoli), 1763. Entomologia Carniolica. Nomen dubium et oblitum. [*Apis*].
?*vesparia* (Gmelin), 1790. *In*: Linnaeus, C. Systema Naturae, ed. 13a, p. 2788. Nomen novum for *vespiformis* (Forster). [*Apis*].
flavilabris Morawitz, 1875. Izv. Imp. Obshch. Ljubrit. Estest. Antrop. Etnogr. 19(2): 158. Southwest Asia (Turkestan).
nuptialis Noskiewicz, 1930. Polskie Pismo Entomol. 9: 261.
varipes Pérez, 1913. Bol. R. Soc. Española Hist. Nat. 13: 332.
flavoguttata flavoguttata (Kirby), 1802. Monographia Apum Angliae, v. 2, p. 215 [*Apis*]. Widespread in Palearctic.
alfkeni Cockerell, 1907 (nec Gaunitz, 1935; nec Noskiewicz, 1939). Ann. Mag. Nat. Hist.(7)20: 131 (nomen novum for *pygmaea* Schenck,1874, nec Cresson, 1863.)
flavoguttata var. *hoeppneri* Alfken, 1898. Entomol. Nachr. 24: 158. Emendation according to ICZN, Article 32d.i(3).
flavoguttata var. *höppneri* Alfken, 1898. Entomol. Nachr. 24: 158.
flavoguttata var. *serotina* Schmiedeknecht, 1882. Apidae Europaeae 1: 190.
minuta Fabricius, 1805 (nec Swenk, 1913). Systema Piezatorum, p. 394.
nana Schenck, 1874. Berliner Entomol. Zeitschr. 18: 343.
pygmaea Schenck, 1874 (nec Cresson, 1863). Berliner Entomol. Zeitschr. 18: 342.
rufocincta (Kirby), 1802. Monographia Apum Angliae, v. 2, p. 216 [*Apis*].
flavoguttata japonensis Tsuneki, 1973. Etizenia 66(2): 115-119. Japan (Hokkaido, Honshu).
flavopicta albopicta Morawitz, 1894. Central Asia (Turkestan, Siberia).
jacobaeae var. *albopicta* Morawitz, 1894. Hor. Soc. Entomol. Ross. 28: 58.
flavopicta flavopicta (Kirby), 1802. Monographia Apum Angliae , v.2, p. 202 [*Apis*]. Widespread in Palearctic.
jacobaeae var. *haematodes* Schmiedeknecht, 1882. Apidae Europaeae 1: 91.
?*jacobaeae* var. *konowiana* Friese, 1921. Deutsche Entomol. Zeitschr. 1920: 252.
jacobaeae var. *miranda* Schmiedeknecht, 1882. Apidae Europaeae 1: 91.
?*jacobaeae* var. *parva* Friese, 1921 (nec *parva* Robertson, 1900). Deutsche Entomol. Zeitschr. 1920: 252.
jasnitskii Cockerell, 1928. Ann. Mag. Nat. Hist.(10)1: 348.
**floricola* Tsuneki, 1973. Etizenia 66 (1): 78. Japan (Honshu).
**florilega* Lovell & Cockerell, 1905. Psyche 12: 41. Eastern and central U.S.
**fontis* Cockerell, 1910. Canadian Entomol. 42: 367. Western U.S. (Colorado).
fragariae Mitchell, 1962. North Carolina Agr. Expt. Sta. Tech. Bull. 152: 391. Southeastern U.S.
fragilis fragilis Cresson, 1878. Trans. American Entomol. Soc. 7: 79. Western U.S.
fragilis mesosticta Cockerell, 1939. Ann. Mag. Nat. Hist. (11) 3: 182. Western U.S. (California).
frankei Cockerell, 1929. Jour. New York Entomol. Soc. 37: 443. Western U.S. (Colorado).
fukuiana Tsuneki, 1973. Etizenia 66 (1): 75. Japan (Honshu).
fulvicornis fulvicornis Fabricius, 1793. Entomologia Systematica, v. 2, p. 348. Throughout Palearctic (Britain to Japan).
?*aurantiaca* Morawitz, 1875. Izv. Imp. Obshch. Ljubrit. Estest. Antrop. Etnogr. 19(2): 156.
belikovi Cockerell, 1928. Ann. Mag. Nat. Hist. (10)1: 348.
capreae (Kirby), 1802. Monographia Apum Angliae, v. 2, p. 193 [*Apis*].
cornigera (Kirby), 1802. Monographia Apum Angliae, v. 2, p. 190 [*Apis*].
lineola Panzer, 1798. Fauna Insectorum Germanicae, Heft 53, p. 23.
lineola var. *aurigera* Schmiedeknecht, 1882. Apidae Europaeae 1: 64, 67.
lineola var. *aurolimbata* Lozinski, 1922. Bull. Int. Acad. Polonaise Sci. Let. Cl. Sci. Math. Nat. Ser. B 1921: 99.
lineola var. *bremensis* Alfken, 1913. Abhandl. Naturwis. Ver. Bremen 22: 101.
lineola var. *brunneofasciata* Lozinski, 1922. Bull. Int. Acad. Polonaise Sci. Let. Cl. Sci. Math. Nat. Ser. B 1921: 100.
lineola var. *decorata* Markowsky, 1939 (nec decorata Smith, 1854). Mitt. Deutsche Entomol. Ges. 9: 66.
lineola var. *diluta* Gribodo, 1893 (nec *diluta* Pérez, 1884). Bull. Soc. Entomol. Italiana 25:426.
lineola var. *erubescens* Friese, 1921. Deutsche Entomol. Zeitschr. 1920: 251.
lineola var. *eversmanni* Lozinski, 1922. Bull. Int. Acad. Polonaise Sci. Let. Cl. Sci. Math. Nat. Ser. B 1921: 101.
lineola var. *flavolimbata* Schmiedeknecht, 1882. Apidae Europaeae 1: 68.

lineola var. *latistriga* Schmiedeknecht , 1882. Apidae Europaeae 1: 64.
lineola var. *melanocera* Gribodo, 1893. Bull. soc. Entomol. Ital. 25: 427.
lineola var. *melanothorax* Schmiedeknecht, 1882. Apidae Europaeae 1: 66.
lineola var. *meridionalis* Schmiedeknecht, 1882. Apidae Europaeae 1: 64.
lineola var. *nigrina* Lozinski, 1922. Bull. Int. Acad. Polonaise Sci. Let. Cl. Sci. Math. Nat. Ser. B 1921: 99.
lineola var. *quadrivittata* Lozinski, 1922. Bull. Int. Acad. Polonaise Sci. Let. Cl. Sci. Math. Nat. Ser. B 1921: 101.
lineola var. *rossica* Schmiedeknecht, 1882. Apidae Europaeae 1: 65.
lineola var. *rufomaculata* Lozinski, 1922. Bull. Int. Acad. Polonaise Sci. Let. Cl. Sci. Math. Nat. Ser. B 1921: 100.
lineola var. *sagemehli* Schmiedeknecht, 1882. Apidae Europaeae 1: 66.
lineola var. *sagemehlii* Dalla Torre, 1896. Catalogus Hymenopterorum, v. 10, p. 356. Emendation.
lineola var. *sibirica* Mocsáry, 1901. Zichy. Ergebn. 2: 167.
?*rakosiensis* Friese, 1921. Deutsche Entomol. Zeitschr. 1920: 255.
schmiedeknechti Schmiedeknecht, 1882. Apidae Europaeae 1: 172.
sexcincta (Kirby), 1802. Monographia Apum Angliae, v. 2, p. 198 [*Apis*].
subcornuta (Kirby), 1802. Monographia Apum Angliae, v. 2, p. 192 [*Apis*].
ventralis Imhoff, 1834. Isis 1834: 374.

fulvicornis jezoensis Matsumura, 1912. Japan (Honshu).
jezoensis Matsumura, 1912. Thousand Insects of Japan, Suppl. 4: 196.

fulvicornis maroccana Pérez, 1895. Northwest Africa (Morocco).
maroccana Pérez, 1895. Espèces Nouvelles de Mellifères de Barbarie, p. 30.
pintosi Dusmet, 1915. Mem. R. Soc. Española Hist. Nat. 8 (Mem. 7): 310.

fulvicornis robusta Morawitz, 1870. Eastern Europe (Hungary, Russia).
punctata Smith, 1854 (nec Lepeletier, 1841). Catalogue of Hymenopterous Insects in the Collection of the British Museum, v. 2, p. 241. Nomen novum for *rubra* Eversmann, 1852 (nec Smith, 1849).
punctigera Dalla Torre, 1896. Catalogus Hymenopterorum, v. 10, p. 361. Nomen novum for *punctata* Smith (nec Fabricius, 1793; nec Lepeletier, 1841).
robusta Morawitz, 1870. Hor. Soc. Entomol. Ross. 7: 326.
rubra Eversmann, 1852. (nec Geoffrey, 1785; nec Provancher, 1888; nec Smith, 1849). Bull. Soc. Imp. Nat. Moscou 25: 100.

fulvicornis strigicollis Morawitz, 1875. Turkestan.
strigicollis Morawitz, 1875. Izv. Imp. Obshch. Ljubrit. Estest. Antrop. Etnogr. 19(2): 155.

fusca Schwarz, 1986. Entomofauna 7: 434. Sweden, Finland, Estonia, western Russia.

fuscicincta Swenk, 1915. Univ. Stud. (Lincoln, Nebraska) 15: 178. North-central U.S. (North Dakota).

gibbosa Viereck, 1905. Canadian Entomol. 37: 285. Northwestern U.S. (Oregon).

gillettei Cockerell, 1905. Bull. Colorado Agr. Expt. Sta. 94: 81. Western U.S. (Colorado).

glabriventris Schwarz, 1990. Entomofauna, Supplement 5: 9. India.

gracilicornis Morawitz, 1895. Hor. Soc. Entomol. Ross. 29: 48. Turkmenistan (Koppeh Dagh), Turkey, Israel.

gracilis Cresson, 1863. Proc. Entomol. Soc. Philadelphia 2: 295. Northeastern U.S.

**graenicheri* Cockerell, 1905. Canadian Entomol. 37: 189. North-central U.S. (Wisconsin).

gransassoi Schwarz, 1986. Entomofauna 7: 438. Central Europe (Swiss Alps, Abruzzi Mts.).

**grayi eastonensis* Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 597. Northwestern U.S. (Washington).

**grayi grayi* Cockerell, 1903. Ann. Mag. Nat. Hist. (7)12: 203. Northwestern U.S. (Oregon).

gribodoi Schmiedeknecht, 1882. Apidae Europaeae 1: 96. Southern Europe, northwest Africa.
basalis Pérez, 1895 (nec Herrich-Schäffer, 1839). Espèces Nouvelles de Mellifères de Barbarie, p. 30.
dispar Pérez, 1895. Espèces Nouvelles de Mellifères de Barbarie, p. 65. Nomen novum for *basalis* Pérez, 1895.
elegans Mocsáry, 1897. Termes. Fuzetek 20: 646.

guttulata Schenck, 1859. Jahrb. Ver. Naturk. Nassau 14: 391. Widespread in Palearctic.
rufilabris Thomson, 1870. Opuscula Entomologica, P.2: 95.

gyangensis Cockerell, 1911. Entomologist 44: 176. Tibet.

?*hackoda* Tsuneki, 1973. Etizenia 66 (2): 128. Japan (northern Honshu).

hakodatensis Tsuneki, 1976. Kontyu 44: 52. Japan (Hokkaido).

hakonensis Cockerell, 1911. Proc. U. S. Natl. Mus. 39: 647. Japan (Hokkaido, Honshu).

hammarstroemi Morawitz, 1888. Hor. Soc. Entomol. Ross. 22: 254. Russia (Siberia).

?*hanedai* Tsuneki, 1976. Kontyu 44: 58. Japan (Honshu).

harimensis Cockerell, 1914. Ann. Mag. Nat. Hist. (8)13: 425 (male, not female). Japan (Hokkaido, Honshu, Kyushu).
orientalis Yasumatsu & Hirashima, 1953. Kontyu 20: 29.

**heterosticta* Cockerell, 1921. American Mus. Novitates 24: 9. Northwestern U.S. (Idaho).

?*hiackogawa* Tsuneki, 1973. Etizenia 66 (2): 134. Japan (Hokkaido, northern Honshu).

hirtipes Pérez, 1884. Act. Soc. Linn. Bordeaux 37: 349. Northern and central Europe.
bucephalae Perkins, 1917. Entomol. Mon. Mag. 53: 12.

hispanica Dusmet, 1913. Mem. R. Soc. Española Hist. Nat. 9: 390. Spain.
nuptura Dusmet, 1913. Mem. R. Soc. Española Hist. Nat. 9: 391.

**hoodiana* Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 608. Northwestern U.S. (Oregon).

?*hummeli* Alfken, 1936. Ark. Zool. 27A no. 37: 15. Southern Mongolia.

hungarica Dalla Torre & Friese, 1894. Entomol. Nachr. 20: 40. Nomen novum for *scita* Schmiedeknecht, 1882 (nec Cresson, 1878). Hungary, Russia.
scita Schmiedeknecht, 1882. Apidae Europaeae 1: 135. Preoccupied.

hydrophylli Swenk, 1915. Univ. Stud. (Lincoln, Nebraska) 15: 179. Eastern and central U.S.

ibanezi Dusmet , 1915. Mem. R. Soc. Española Hist. Nat. 8 (Mem. 7): 316. North Africa (Morocco).
velardei Dusmet, 1915. Mem. R. Soc. Española Hist. Nat. 8 (Mem. 7): 322.

?**icazti* Tsuneki, 1976. Kontyu 44: 59. Japan (Honshu).

idahoensis Swenk, 1913. Univ. Stud. (Lincoln, Nebraska) 12: 53. Northwest U.S. (Idaho).

illinoensis Robertson, 1900. Canadian Entomol. 32: 294. Eastern and central U.S.
illinoiensis Robertson, 1903. Canadian Entomol. 35: 178, 179. (Lapsus calami).
illinoënsis Cockerell, 1921. American Mus. Novitates 24: 7. Emendation (unjustified).

**imbricata* Smith, 1854. Catalogue of the Hymenoptera in the Collection of the British Museum, v.2, p. 246. .Northeastern North America.

indusata Mitchell, 1962. North Carolina Agr. Expt. Sta. Tech Bull. 152: 418. Southeastern U.S. (North Carolina, Georgia).

**inepta* Mitchell, 1962. North Carolina Agr. Expt. Sta. Tech Bull. 152: 419. Eastern and central U.S.

inermis Pérez, 1895 (nec Friese, 1921). Espèces Nouvelles de Mellifères de Barbarie, p. 31. Northwest Africa.

integerrima Dalla Torre, 1896. Catalogus Hymenopterorum, v. 10, p. 353. Nomen novum for *integra* Robertson, 1893 (nec Brullé, 1832; nec Imhoff, 1834). Central and eastern N. America.

integra Robertson, 1893. Trans. American Entomol. Soc. 20: 276. Preoccupied.

integer Robertson, 1903. Canadian Entomol. 35: 177. Lapsus calami.

interruptella Fowler, 1902. Rep. California Agr. Expt. Sta., 1898-1901, p. 329. Nomen novum for *interrupta* Fowler, 1899 (nec Panzer, 1798). Western U.S. (California).

interrupta Fowler, 1899. Entomol. News 10: 159. Preoccupied.

italica Dalla Torre & Friese, 1894. Entomol. Nachr. 20: 40. Nomen novum for *festiva* Schmiedeknecht, 1882 (nec Cresson, 1863). Southern and central Europe, southwest Asia.

festiva Schmiedeknecht, 1882. Apidae Europaeae 1: 77. Preoccupied.

**itamera* Cockerell, 1910. Psyche 17: 95. Northwestern U.S. (Washington).

**jammuensis* Schwarz, 1990. Entomofauna, Supplement 5: 20. North India/Pakistan (Kashmir).

jennei Cockerell, 1906. Canadian Entomol. 38: 281. Northwestern U.S. (Washington).

**jocularis* Cresson, 1879. Trans. American Entomol. Soc. 7: 202. Western U.S. (Nevada).

kaguya Hirashima, 1953. Trans. Shikoku Entomol. Soc. 3: 135. Japan (Honshu).

kervilleana Pérez, 1913. Bull. Soc. Amis Sci. Nat. Rouen 47: 77. Syria, Israel, Turkey.

**kincaidiana* Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 614. Northwestern U.S. (Washington).

**kingstonensis* Mitchell, 1962. North Carolina Agr. Expt. Sta. Tech. Bull. 152: 420. Northeastern U.S. (Rhode Island).

?**kinosukei* Tsuneki, 1973. Etizenia 66 (2): 121. Japan (Honshu).

?*klamathensis* Fox, 1926. Pan-Pac. Entomol. 2: 212. Northwestern U.S. (Oregon).

koebelei Cockerell, 1911. Proc. U.S. Natl. Mus. 39: 645. Japan.

miensis Tsuneki, 1973. Etizenia 66 (1): 73.

komarowi Radoszkowski, 1893. Hor. Soc. Entomol. Ross. 27: 55. Central Asia.

semenowi Morawitz, 1895. Hor. Soc. Entomol. Ross. 29: 52.

koreana Cockerell, 1926. Pan-Pac. Entomol. 3: 88. Korea.

koreana Tsuneki, 1986. Spec. Publ. Japan Hymen. Assoc. 32: 33. Korea (junior homonym).

kornosica Mavromoustakis, 1958. Beitr. Entomol. 8: 217. Cyprus.

?**kotomaria* Tsuneki, 1986. Spec. Publ. Japan Hymen. Assoc. 32: 51. Japan (northern Honshu).

krombeini Schwarz, 1966. Nachr. Bayerischen Entomol. 15: 24. Nomen novum for *propinqua* Swenk, 1913 (nec Schmiedeknecht, 1882). Central U.S. (Nebraska).

propinqua Swenk, 1913. Univ. Stud. (Lincoln, Nebraska) 12: 46. Preoccupied.

?**kuro* Tsuneki, 1986. Spec. Publ. Japan Hymen. Assoc. 32: 52. Japan (Honshu).

**ladakhiensis* Schwarz, 1990. Entomofauna, Supplement 5: 17. India.

laramiensis Swenk, 1913. Univ. Stud. (Lincoln, Nebraska) 12: 75. Western U.S. (Wyoming).

lathburiana (Kirby), 1802. Monographia Apum Angliae, v. 2, p. 183. Widely distributed in Palearctic [*Apis*].

rufiventris (Kirby), 1802. Monographia Apum Angliae, v. 2, p. 187 [*Apis*].

**latifrons* Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 572. Western U.S. (California, Nevada).

lehighensis Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 605. Eastern and central North America.

lepida Cresson, 1863. Proc. Entomol. Soc. Philadelphia 2: 288. Eastern and central North America.

leucophthalma (Kirby), 1802. Monographia Apum Angliae, v. 2, p. 197 [*Apis*]. Northern and central Europe.

borealis Zetterstedt, 1838. Insecta Lapponica Descripta, v. 1, p. 470.

inquilina Smith, 1844. Zoologist 2: 605.

leucozona Rodeck, 1931. American Mus. Novitates 496: 4. Western U.S. (Colorado).

**lewisi* Cockerell, 1903. Ann. Mag. Nat. Hist. (7)12: 205. Northwest U.S. (Oregon).

libata Cresson, 1878. Trans. American Entomol. Soc. 7: 80. Western U.S. (Colorado).

limbata Dalla Torre, 1896. Catalogus Hymenopterorum, v. 10, p. 354 (Lapsus calami).

litigiosa Gribodo, 1893. Bull. Soc. Entomol. Italiana 25: 419. Algeria, Sicily.

**louisianae* Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 602. Eastern and central U.S.

?*lutea* Eversmann, 1852. Bull. Soc. Imp. Nat. Moscou 25: 96. Southeastern Europe, Russia.

fasciculata Morawitz, 1888. Hor. Soc. Imp. Entomol. Ross. 22: 259.

?*luteola* Olivier, 1811. Encyclopédie Méthodique. Dictionnaire des Insectes, v. 8, p. 365. Eastern U.S. (type lost or destroyed?).

**luteoloides* Robertson, 1895. Trans. American Entomol. Soc. 22: 124. Eastern U.S.

luteopicta Cockerell, 1905. Bull. Colorado Agr. Expt. Sta. 94: 83. Western U.S. (Colorado).

maculata Cresson, 1863. Proc. Entomol. Soc. Philadelphia 2: 303. Central and eastern U.S.

volatilis Smith, 1879. Descriptions of New Species of Hymenoptera in the Collection of the British Museum, p. 100.

maculicornis Pérez, 1884. Act. Soc. Linn. Bordeaux 37: 352. Southern France, Spain.

maculifrons Smith, 1869. Entomologist 4: 206. Japan (Hokkaido, Honshu).

maculipennis (Cameron), 1902 (nec Friese, 1923). Jour. Bombay Nat. Hist. Soc. 14: 419. Northern India (Simla). [*Lamproapis*].

?*maculipennis* Friese, 1923 (nec Cameron, 1902). *In:* Friese and von Schulthess, 1923. Konowia 2: 279. Libya. (secondary junior homonym).

maculiventer Swenk, 1915. Univ. Stud. (Lincoln, Nebraska) 15: 163. North-central U.S. (North Dakota).

?*malonella* Cockerell, 1910. Psyche 17: 93. Northwestern U.S. (Washington).

?*mamiyai* Tsuneki, 1976. Kontyu 44: 54. Japan (Hokkaido).

margelanica Schwarz, 1987. Entomofauna 8: 460. Central Asia (Uzbekistan, Kazakhstan).

marshamella (Kirby), 1802. Monographia Apum Angliae, v. 2, p. 188. Widespread in Palearctic [*Apis*].

marshamella var. *dubia* Schmiedeknecht, 1882. Apidae Europaeae 1: 72, 74.

marshamella var. *modesta* Schmiedeknecht, 1882 (nec *modesta* Cresson, 1863; nec *modesta* Herrich-Schäffer, 1839). Apidae Europaeae 1: 71, 73.

media Mitchell, 1962. North Carolina Agr. Expt. Sta. Tech. Bull. 152: 421. Southeastern U.S. (Tennessee, North Carolina).

**mediana* Swenk, 1913. Univ. Stud. (Lincoln, Nebraska) 12: 49. Western U.S. (California, Oregon).

melanura Mocsáry, 1883 (nec Tsuneki, 1973). Magy. Akad. Természet. Értek. 13: 62. Northwest Africa.

gonzalezi Dusmet, 1915. Mem. R. Soc. Española Hist. Nat. 8 (Mem. 7): 314.

gracilipes Pérez, 1902. Proc.-Verb. Soc. Linn. Bordeaux 57:lx.

palaciosi Dusmet, 1915. Mem. R. Soc. Española Hist. Nat. 8 (Mem. 7): 314.

melathoracica Imhoff, 1834. Isis 1834: 373.

freygessneri Schmiedeknecht, 1882. Apidae Europaeae 1: 23, 102.

mendica Mitchell, 1962. North Carolina Agr. Expt. Sta. Tech. Bull. 152: 422. Northeast U.S. (Vermont, New Hampshire).

micronycha Pérez, 1902. Proc.-Verb. Soc. Linn. Bordeaux 57: lxiii. Locality not reported.

**miniata* Smith, 1854. Catalogue of the Hymenoptera in the Collection of the British Museum, v. 2, p. 250. Southeastern U.S. (Georgia).

?*minima* Mitchell, 1962. North Carolina Agr. Expt. Sta. Tech. Bull. 152: 423. Eastern U.S. (Maryland to North Carolina).

?*minor* Gmelin, 1790. *In* Linnaeus. Systema Naturae, ed. 13a, p. 2796.

?*mishimana* Tsuneki, 1976. Kontyu 44: 154. Japan (Honshu).

moeschleri Alfken, 1913. Northern and central Europe. Emendation according to ICZN, Article 32d.i(3).

bifida var. *möschleri* Alfken, 1913. Heimat Kiel 53: 147.

?*montverna* Tsuneki, 1973. Etizenia 66 (2): 119. Japan (Honshu).

**morrisoni flagellaris* Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 587. Western U.S. (Colorado).

**morrisoni morrisoni* Cresson, 1878. Trans. American Entomol. Soc. 7: 72. Western U.S. (Colorado).

?**muinensis* Tsuneki, 1986. Spec. Publ. Japan Hymen. Assoc. 32: 56. Japan (Hokkaido).

**munda* Cresson, 1878. Trans. American Entomol. Soc. 7: 80. Western U.S. (Colorado).

?**murotai* Tsuneki, 1973. Etizenia 66 (2): 110. Japan (Honshu).

mutica Morawitz, 1872. Verh. Zool. Bot. Ges. Wien 22: 380. Southern and central Europe.

cincta Lepeletier, 1841 (nec Rossi, 1792; nec Herrich-Schäffer, 1839). Histoire Naturelle des Insectes, Hyménoptères, v. 2, p. 484.

olympica Schmiedeknecht, 1882. Apidae Europaeae 1: 176.

?*mutsuensis* Tsuneki, 1986. Spec. Publ. Japan Hymen. Assoc. 32: 53. Japan (Honshu).

?*nanaensis* Tsuneki, 1973. Etizenia 66 (2): 131. Japan (Hokkaido).

**nigrociliata* Swenk, 1913. Univ. Stud. (Lincoln, Nebraska) 12: 32. West-central U.S. (Nebraska).

**nigrocincta* Smith, 1879. Descriptions of New Species of Hymenoptera in the Collection of the British Museum, p. 99. Northern U.S. (Maine, Oregon).

**nigrofasciata* Swenk, 1913. Univ. Stud. (Lincoln, Nebraska) 12: 24. West-central U.S. (Nebraska).

noskiewiczi Schwarz, 1966. Nachr. Baverischen Entomol. 15: 24. Nomen novum for *alfkeni* Noskiewicz, 1939 (nec Cockerell, 1907; nec Gaunitz, 1935). Eastern Europe (Hungary).

alfkeni Noskiewicz, 1939. Polskie Pismo Entomol. 16-17: 257. Preoccupied.

?*nurukawa* Tsuneki, 1973. Etizenia 66 (2): 135. Japan (northern Honshu).

obburdinensis Morawitz, 1875. Izv. Imp. Obshch. Ljubrit. Estest. Antrop. Etnogr. 19(2): 157. Central Asia (Turkestan, Kashmir).

obliquella Fowler, 1902. Rep. California Agr. Expt. Sta., 1898-1901, p. 329. Nomen novum for *obliqua* Fowler, 1899 (nec Olivier, 1811). Western U.S. (California).

obliqua Fowler, 1899. Entomol. News 10: 160. Preoccupied.

obliterata Cresson, 1863. Proc. Entomol. Soc. Philadelphia 2: 301. Eastern and central U.S.

?*pulchella* Smith, 1854. Catalogue of the Hymenoptera in the Collection of the British Museum, v. 2, p. 247.

viburni Robertson, 1897. Trans. Acad. Sci. St. Louis 7: 341.

obscura Zetterstedt, 1838. Insecta Lapponica Descripta, v. 1, p. 470. Northern and central Europe.

obscura var. *alfkeni* Gaunitz, 1935 (nec Cockerell, 1907; nec Noskiewicz, 1939). Entomol. Tidskr. 56: 96.

obscura var. *bitincta* Alfken, 1924. Notul. Entomol. 4: 37.

obscurella Fowler, 1902. Rep. California Agr. Expt. Sta., 1898-1901: 329. Nomen novum for *obscura* Fowler, 1899 (nec Zetterstedt, 1838). Western U.S. (California, Oregon).

obscura Fowler, 1899. Entomol. News 10: 160. Preoccupied.

fowleri Cockerell, 1903. Ann. Mag. Nat. Hist. (7) 12: 204.

?**obscuriventris* Schwarz, 1990. Entomofauna, Supplement 5: 22. Nepal.

**obtusata* Swenk, 1915. Univ. Stud. (Lincoln, Nebraska) 15: 159. North-central U.S. (North Dakota). Emendation (see Hurd, 1979, p. 2100).

obstusata Swenk, 1915. Univ. Stud. (Lincoln, Nebraska) 15: 159 (Lapsus calami).

ochlerata Mitchell, 1962. North Carolina Agr. Expt. Sta. Tech. Bull. 152: 396. North-central U.S. (Michigan).

**ochrohirta* Swenk, 1913. Univ. Stud. (Lincoln, Nebraska) 12: 34. West-central U.S. (Nebraska).

odontocera Cockerell, 1916. Pomona Coll. Jour. Entomol. Zool. 8: 57. Western U.S. (California).

?**ohnonis* Tsuneki, 1976. Kontyu 44: 61. Japan (Honshu).

opaca Alfken, 1913. Southern and central Europe.

bifida var. *opaca* Alfken, 1913. Abhandl. Naturwis. Ver. Bremen 22: 105.

opacella Timberlake, 1954. Pan-Pac. Entomol. 30: 133. Western U.S. (California).

**opposita* Cresson, 1878. Trans. American Entomol. Soc. 7: 73. Western U.S. (California).

orba Mitchell, 1962. North Carolina Agr. Expt. Sta. Tech. Bull. 152: 424. Northeastern U.S. (New York).

?**orcusella* Cockerell, 1910. Psyche 17: 95. Northwestern U.S. (Washington).

oregonica Cockerell, 1903. Ann. Mag. Nat. Hist. (7) 12: 205. Northwestern U.S. (California, Oregon).

ornithica Cockerell, 1906. Canadian Entomol. 38: 161. Western U.S. (Colorado).

orophila Cockerell, 1921. American Mus. Novitates 24: 8. Western U.S. (Colorado, Wyoming).

osborni Cockerell, 1911. Proc. U. S. Natl. Mus. 41: 243. Southwestern U.S. (Arizona).

?*osimana osimana* Tsuneki, 1973. Etizenia 66 (2): 129. Japan (Hokkaido).

?*osimana oirasensis* Tsuneki, 1973. Etizenia 66 (2): 131. Japan (northern Honshu).

shimoyamai Tsuneki, 1973. Etizenia 66 (2): 137.

ovata (Robertson), 1903. Canadian Entomol. 35: 175. Eastern and central U.S. [*Gnathias*].

carolinae Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 602.

Gnathias ovatus form *binotatus* Robertson, 1903. Canadian Entomol. 35: 175.

Gnathias ovatus form *octomaculatus* Robertson, 1903. Canadian Entomol. 35: 175.

Gnathias ovatus form *plenus* Robertson, 1903. Canadian Entomol. 35: 175.

Gnathias ovatus form *quadrimaculatus* Robertson, 1903. Canadian Entomol. 35: 175.

Gnathias ovatus form *sexmaculatus* Robertson, 1903. Canadian Entomol. 35: 175.

Gnathias ovatus form *unicolor* Robertson, 1903. Canadian Entomol. 35: 175.

pacifica Tsuneki, 1973. Etizenia 66 (2): 97. Japan (Honshu).

**packardiella* Cockerell, 1906. Ann. Mag. Nat. Hist. (7) 17: 225. Western U.S. (Colorado, Washington?).

pallidella Cockerell, 1905. Bull. Colorado Agr. Expt. Sta. 94: 82. Western U.S. (Colorado).

pallidenotata Schmiedeknecht, 1882. Apidae Europaeae 1: 140. Southern Russia.

pallidipicta Swenk, 1913. Univ. Stud. (Lincoln, Nebraska) 12: 48. West-central U.S. (Nebraska).

panzeri panzeri Lepeletier, 1841. Histoire Naturelle des Insectes, Hyménoptères, v. 2, p. 501. Widespread in Palearctic.

diluta Pérez, 1884 (nec Gribodo, 1893). Act. Soc. Linn. Bordeaux 37: 354.

glabella Thomson, 1870. Opuscula Entomologica, v. 2, p. 96.

Note: *panzeri* Lep. has often been confused with *ruficornis* (L.), so synonyms are very difficult to determine accurately from the literature alone. The following taxa that have been treated as "varieties" of *ruficornis* may be synonyms of *panzeri*. Note that the

two names from Herrich-Schäffer and the name from Geoffrey are older than *panzeri* Lepeletier, although they are younger than *ruficornis* Linnaeus. These names are here regarded as nomina dubia.

?*affinis* Herrich-Schäffer, 1839. Zeitschr. Entomol. 1: 286. Nomen dubium.

?*modesta* Herrich-Schäffer, 1839. (nec Cresson, 1863; nec Schmiedeknecht, 1882). Zeitschr. Entomol. 1: 282. Nomen dubium.

ruficornis var. *fasciata* Friese, 1921. Deutsche Entomol. Zeitschr. 1920: 254.

ruficornis var. *hybrida* Schmiedeknecht, 1882. Apidae Europaeae 1: 166, 167.

ruficornis var. *incompleta* Schmiedeknecht, 1882. Apidae Europaeae 1: 166.

ruficornis var. *phoenicia* Schmiedeknecht, 1882. Apidae Europaeae 1: 165.

?*rubra* (Geoffrey) 1785. (nec Smith, 1849; nec Eversmann, 1852; nec Provancher, 1888). In: Fourcroy. Entomol. Paris 2: 438 [*Vespa*]. Nomen dubium.

panzeri orientis Tsuneki, 1973. Etizenia 66 (1): 68. Japan.

parallela Swenk, 1913. Univ. Stud. (Lincoln, Nebraska) 12: 36. West-central U.S. (Nebraska).

**parata* Cresson, 1878. Trans. American Entomol. Soc. 7: 81. Western U.S. (Colorado).

parva Robertson, 1900. Canadian Entomol. 32: 294. Eastern and central U.S.

infantula Cockerell, 1907. Entomologist 40: 98.

pastoralis Eversmann, 1852 (nec Schmiedeknecht, 1882). Bull. Soc. Imp. Nat. Moscou 25: 101. Albania, Asia Minor, Ural Mts., Siberia.

perbella (Viereck), 1905. Canadian Entomol. 37: 282. Northwestern North America (Oregon, Washington, British Columbia). [*Gnathias*].

**perivincta perivincta* Cockerell, 1905. Bull. Colorado Agr. Expt. Sta. 94: 80. Western U.S. (Colorado).

**perivincta semirufula* Cockerell, 1905. Western U.S. (Colorado).

perivincta var. *semirufula* Cockerell, 1905. Bull. Colorado Agr. Expt. Sta. 94: 80.

perplexa Cresson, 1863. Proc. Entomol. Soc. Philadelphia 2: 306. Central and eastern U.S., ?Wyoming.

cornelliana Cockerell, 1908. Proc. Entomol. Soc. Washington 10: 84.

perplexans Cockerell, 1910. Psyche 17: 94. Northwestern U.S. (Washington).

physura Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 599. Western U.S. (Nevada).

piccioliana Magretti, 1883. Ann. Soc. Entomol. France (6)3: 206. Southern Europe.

novioregensis Pérez, 1902. Proc.-Verb. Soc. Linn. Bordeaux 57: lx.

jurassica Stöckhert, 1941. Mitt. Münchner Entomol. Ges. 31: 1078.

piliventris Morawitz, 1877. Hor. Soc. Entomol. Ross. 14: 110. Asia Minor, Caucasus

**placitensis* Cockerell, 1903. Ann. Mag. Nat. Hist. (7)12: 446. Southwestern U.S. (New Mexico).

platythorax Schwarz, 1981. Entomofauna 2: 363. Turkey, Hungary.

platyventris Morawitz, 1886. Hor. Soc. Entomol. Ross. 20: 77. Transcaucasus, Turkestan.

propinqua Schmiedeknecht, 1882 (nec Swenk, 1913). Apidae Europaeae 1: 174. Southeast Europe (Greece, Italy, Balkan Peninsula).

proxima Cresson, 1863. Proc. Entomol. Soc. Philadelphia 2: 294. Northeastern U.S. (Maine, ?Connecticut).

**pseudops* Cockerell, 1905. Canadian Entomol. 37: 189. Northeastern and northcentral U.S.

pulchra Arnold, 1888. Hor. Soc. Entomol. Ross. 22: 202. Russia.

olhae Cockerell, 1928. Ann. Mag. Nat. Hist. (10)1: 350.

**pulsatillae* Cockerell, 1906. Ann. Mag. Nat. Hist. (7)18: 69. Western U.S. (Colorado, ?Washington).

pygidialis Schwarz, 1981. Entomofauna 2: 362. Southeastern Europe, Rhodes, Turkey.

pygmaea Cresson, 1863 (nec Schenck, 1874). Proc. Entomol. Soc. Philadelphia 2: 299. Eastern and central U.S., ?Colorado.

pyrifera Cockerell, 1918. Ann. Mag. Nat. Hist. (9)2: 480. Japan (Honshu, Kyushu).

**pyrrha* Cockerell, 1916. Pomona Coll. Jour. Entomol. Zool. 8: 55. Western U.S. (California).

quadrifasciata Schwarz, 1981. Entomofauna 2: 366. Turkey.

radiata Nurse, 1903. Ann. Mag. Nat. Hist. (7)11: 543. North India/Pakistan (Kashmir).

radoszkowskii Łozinski, 1922. Bull. Int. Acad. Polonaise Sci. B 1921: 112. Western Asia (Caucasus).

**rengnio* Tsuneki, 1973. Etizenia 66 (2): 91. Japan (Honshu).

rhenana Morawitz, 1872. Verh. Zool. Bot. Ges. Wien 22: 382. Northwest Africa, western and central Europe, east to Hungary.

rufipes Schenck, 1870 (nec Fabricius, 1793). Jahrb. Ver. Naturk. Nassau (1867-1868) 21/22: 342. Preoccupied.

**rhodalis* Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 600. Western U.S. (Nevada).

rhodomelas Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 598. Northwestern N. America (British Columbia, Oregon).

rhodosoma rhodosoma Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 571. Western U.S. (California, Nevada).

rhodosoma rhodosomella Cockerell, 1903. Western U.S. (Colorado).

rhodosoma var. *rhodosomella* Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 571.

**rhodoxantha* Cockerell, 1905. Bull. Colorado Agr. Expt. Sta. 94: 78. Western U.S.(Colorado).

?*risiriensis* Tsuneki, 1976. Kontyu 44: 50. Japan (Risiri Island, Hokkaido).

rivalis Cresson, 1878. Trans. American Entomol. Soc. 7: 79. Western U.S. (California, Washington).

**robertsonella* Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 613. Western U.S. (Nevada).

?*romana* Friese, 1921. Deutsche Entomol. Zeitschr. 1920: 259. Eastern Europe (Hungary).

rostrata Herrich-Schäffer, 1839 (nec Lepeletier, 1841). Zeitschr. Entomol. 1: 280. Central and southeastern Europe.

eustalacta Gerstäcker, 1869. Stettiner Entomol. Ztg. 30: 164.

longiceps Schmiedeknecht, 1882. Apidae Europaeae 1: 173.

rubi Swenk, 1915. Univ. Stud. (Lincoln, Nebraska) 15: 174. North-central U.S. (North Dakota, Minnesota).

**rubrella* Cockerell, 1905. Bull. Colorado Agr. Expt. Sta. 94: 75. Western U.S. (Colorado).

?**rubrica* Provancher, 1896. Nat. Canadien 23: 8. Western U.S. (California).

rubricosa Eversmann, 1852. Bull. Soc. Imp. Nat. Moscou 25 (3): 100. Russia.

rubriventris Schwarz, 1981. Entomofauna 2: 358. Greece, Bulgaria, Turkey, Turkestan.

ruficollis Morawitz, 1875. Izv. Imp. Obshch. Ljubrit. Estest. Antrop. Etnogr. 19(2): 156. Southwest Asia (Turkestan, Afghanistan, Pakistan).

ruficornis ruficornis (Linnaeus), 1758. Systema Naturae, ed. 10, tomus I, p. 578. Northern and central Europe [*Apis*].

bifida Thomson, 1872. Hymenoptera Scandinaviae, v. 2, p. 196 (also see comments above under *panzeri* Lepeletier).

ruficornis orenbergensis Lozinski, 1922. Western Asia (Russia).

bifida var. *orenburgensis* Lozinski, 1922. Bull. Int. Acad. Polonaise Sci. Let. Cl. Sci. Math. Nat. Ser. B 1921: 111.

ruidosensis Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 594. Western U.S. (Colorado, New Mexico).

sabaensis Tsuneki, 1973. Etizenia 66(2): 112. Japan (Honshu, Hokkaido).

sabulosa Radoszkowski, 1876. Hor. Soc. Entomol. Ross. 12: 121. Algeria, Egypt, Israel.

macrocardia Pérez, 1895. Espèces Nouvelles de Mellifères de Barbarie, p.30.
?*sakura* Tsuneki, 1976. Kontyu 44: 150. Japan (Honshu).
salicicola Swenk, 1913. Univ. Stud. (Lincoln, Nebraska) 12: 35. West-central U.S. (Nebraska).
salicis Robertson, 1900. Trans. Acad. Sci. St. Louis 10: 52. North-central U.S. (Illinois).
sanctaecrucis Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 566. Western U.S. (California).
?*sanguinicollis* Friese, 1921. Deutsche Entomol. Zeitschr. 1920: 261. Southwestern Asia (Caucasus).
?*sarta* Morawitz, 1875. Izv. Imp. Obshch. Ljubrit. Estest. Antrop. Etnogr. 19(2): 154. Southwest Asia (Tadzhikistan).
sayi Robertson, 1893. Trans. American Entomol. Soc. 20: 276. Central and eastern N. America.
schwarzi contractula Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 600. Southwestern U.S. (New Mexico).
schwarzi schwarzi Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 599. Western U.S. (Colorado).
**sedi* Cockerell, 1920. Ann. Mag. Nat. Hist. (9)6: 201. Emendation of *N. sedae* Cockerell, 1919. Western U.S. (Colorado).
sedae Cockerell, 1919. Entomol. News 30: 292.
semirugosa Cockerell, 1929. Ann. Mag. Nat. Hist. (10)4: 297. Western U.S. (Colorado).
shirakii Yasumatsu & Hirashima, 1951. Trans. Shikoku Entomol. Soc. 2: 55. Japan (Honshu, Kyushu).
?*shoyozana* Tsuneki, 1986. Spec. Publ. Japan Hymen. Assoc. 32: 34. South Korea.
siccorum Cockerell, 1919. Entomol. News 30: 291. Western U.S. (Colorado).
signata Jurine, 1807. Nouvelle Méthode de Classer les Hyménoptères, p. 223. Northern and central Europe.
?*ruficornis* var. *herrichschaefferi* Strand, 1917. Arch. Naturg. 82 A2, 1917: 69.
ruficornis var. *mirabilis* Schmiedeknecht, 1882. Apidae Europaeae 1: 164.
silvicola Tsuneki, 1973. Etizenia 66 (2): 87. Japan (Hokkaido, Honshu).
hangani Tsuneki, 1973. Etizenia 66(2): 132.
**siouxensis* Swenk, 1913. Univ. Stud. (Lincoln, Nebraska) 12: 96. West-central U.S. (Nebraska, Wyoming).
**skinneri* Cockerell, 1908. Entomol. News 19: 323. Eastern U.S. (Connecticut to North Carolina).
sobrina Mitchell, 1962. North Carolina Agr. Expt. Sta. Tech. Bull. 152: 431. North-central U.S. (Michigan).
solitaria Smith, 1854. Catalogue of the Hymenoptera in the Collection of the British Museum, v. 2, p 243. Northern India.
decorata Smith, 1854 (nec Markovsky, 1939). Catalogue of the Hymenoptera in the Collection of the British Museum, v. 2, p. 243.
**sphaerogaster* Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 611. Central and eastern U.S. (Wisconsin, New Jersey).
stoeckherti Pittioni, 1951. Central Europe (Austria), southwest Asia (Afghanistan). Emendation according to ICZN, Article 32d.i(3).
stöckherti Pittioni, 1951. Entomol. Nachricht. Österr. Schweizer Entomologen 3: 158.
striata Fabricius, 1793. Entomologia Systematica, v. 2, p. 348. Widespread in Palearctic.
dzieduszyckii Noskiewicz, 1924. Polskie Pismo Entomol. 3: 34.
hillana (Kirby), 1802. Monographia Apum Angliae, v. 2, p. 208 [*Apis*].
ochrostoma (Kirby), 1802 (nec Zetterstedt, 1838). Monographia Apum Angliae, v. 2, p. 209 [*Apis*].
punctiscuta Thomson, 1870. Opuscula Entomologica, v. 2, p. 96.
simillima Pérez, 1913. Bol. R. Soc. Española Hist. Nat. 13: 334.
vidua Smith, 1844. Zoologist 2: 602.
subaccepta Cockerell, 1907. Entomologist 40: 267. Western U.S. (Colorado).
subangusta Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 570. Western U.S. (California).
subgracilis Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 569. Western U.S. (California).
**subnigrocincta* Swenk, 1915. Univ. Stud. (Lincoln, Nebraska) 15: 155. Eastern U.S.
**subpacata* Swenk, 1913. Univ. Stud. (Lincoln, Nebraska) 12: 55. North-central U.S. (North Dakota).
subrubi Swenk, 1915. Univ. Stud. (Lincoln, Nebraska) 15: 176. North-central U.S. (North Dakota).
subrutila Lovell and Cockerell, 1905. Psyche 12: 40. Central and eastern U.S., ?Colorado.
subsimilis Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 567. Western U.S. (California).
subvicinalis Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 576. Western U.S. (California).
**suda* Cresson, 1879. Trans. American Entomol. Soc. 7: 203. Western U.S. (Nevada).
?**sudai* Tsuneki, 1976. Kontyu 44: 152. Japan (Honshu).
**sulphurata* Smith, 1854. Catalogue of the Hymenoptera in the Collection of the British Museum, v. 2, p. 249. Central and eastern U.S., ?Utah.
?*sunayamana* Tsuneki, 1976. Kontyu 44: 63. Japan (Honshu).
swenki Schwarz, 1966. Nachr. Baverischen Entomol. 15: 24. Nomen novum for *minuta* Swenk, 1913 (nec Fabricius, 1805). Central U.S. (Nebraska).
minuta Swenk, 1913. Univ. Studies (Lincoln, Nebraska) 12: 44. Preoccupied.
symphyti Stöckhert, 1930. *In*: Schmiedeknecht. Hymenopteren Nord- und Mitteleuropas, p. 1012.
taraxacella Cockerell, 1903. Western U.S. (Nebraska, Colorado, New Mexico, ?Washington).
ultima taraxacella Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55:589.
tenella Mocsáry, 1883. Magy. Akad. Termész. Értek. 13: 63. Southwestern Asia (Caucasus).
**tintinnabulum* Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 572. Western U.S. (California).
**towada* Tsuneki, 1973. Etizenia 66 (1): 72. Japan (northern Honshu, Hokkaido).
?*townesi* Mitchell, 1962. North Carolina Agr. Expt. Sta. Tech. Bull. 152: 432. Eastern U.S. (Maryland).
trapeziformis Schmiedeknecht, 1882. Central Europe.
ruficornis var. *trapeziformis* Schmiedeknecht, 1882. Apidae Europaeae 1: 165.
ruficornis var. *auctumnalis* Ducke, 1900. Entomol. Nachr. 26: 11.
tricurta Swenk, 1915. Univ. Stud. (Lincoln, Nebraska) 15: 165. North-central U.S. (North Dakota).
truttarum Cockerell, 1909. Entomologist 42: 94. Southwestern U.S. (New Mexico).
**tyrellensis* Mitchell, 1962. North Carolina Agr. Expt. Sta. Tech. Bull. 152: 433. Southeastern U.S. (North Carolina, Florida).
ulsterensis Mitchell, 1962. North Carolina Agr. Expt. Sta. Tech. Bull. 152: 433. Eastern U.S. (New York, District of Columbia).
ultima Cockerell, 1903. Ann. Mag. Nat. Hist. (7)12: 206. Northwestern U.S. (California, Oregon, Washington).
modocorum Cockerell, 1903. Ann. Mag. Nat. Hist. (7)12: 444.
**ultimella septentrionalis* Swenk, 1913. Univ. Stud. (Lincoln, Nebraska) 12: 50. Northwestern U.S. (Washington).
**ultimella ultimella* Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 572. Western U.S. (California).
undulaticornis Cockerell, 1906. Ann. Mag. Nat. Hist. (7)18: 70. Western U.S. (Colorado).
utensis Swenk, 1913. Univ. Stud. (Lincoln, Nebraska) 12: 97. Western U.S. (Colorado).
?**uzensis* Tsuneki, 1986. Spec. Publ. Japan Hymen. Assoc. 32: 49. Japan (Honshu).

**valida* Smith, 1854. Catalogue of the Hymenoptera in the Collection of the British Museum, v. 2, p. 246. Northern North America (Nova Scotia and New York to British Columbia).
**vallesina honorata* Cockerell, 1922. Western U.S. (Colorado).
vallesina var. *honorata* Cockerell, 1922. Ann. Mag. Nat. Hist. (9)10: 269.
**vallesina vallesina* Cockerell, 1906. Ann. Mag. Nat. Hist. (7)17: 226. Western U.S. (Colorado, New Mexico).
**velutina* Swenk, 1913. Univ. Stud. (Lincoln, Nebraska) 12: 39. West-central U.S. (Nebraska).
verna Schmiedeknecht, 1882. Apidae Europaeae 1: 110. Eastern Europe.
balteata Schmiedeknecht, 1882. Apidae Europaeae 1: 185.
?*vernalis* Morawitz, 1875. Izv. Imp. Obshch. Ljubrit. Estest. Antrop. Etnogr. 19(2): 152. Southwest Asia (Tashkent, Uzbekistan).
vernonensis Cockerell, 1916. Canadian Entomol. 48: 273. Western Canada (British Columbia).
vexator Cockerell, 1909. Entomologist 42: 92. Western U.S. (Colorado).
vicina stevensi Swenk, 1913. Univ. Stud. (Lincoln, Nebraska) 12: 56. North-central U.S. (North Dakota).
vicina vicina Cresson, 1863. Proc. Entomol. Soc. Philadelphia 2: 292. Eastern and central N. America.
vicinalis infrarubens Cockerell, 1905. Western U.S. (Oregon).
vicinalis var. *infrarubens* Cockerell, 1905. Bull. Colorado Agr. Expt. Sta. 94: 84.
vicinalis vicinalis Cresson, 1878. Trans. American Entomol. Soc. 7: 78. West-central U.S. (Nebraska, Colorado).
villosa Thomson, 1870. Opuscula Entomologica, v.2, p. 95. Northern Europe (Sweden).
**vulpis* Cockerell, 1921. American Mus. Novitates 24: 10. Western U.S. (Wyoming).
?*wakasana* Tsuneki, 1976. Kontyu 44: 56. Japan (Honshu).
**washingtoni* Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 598. Northwestern U.S. (Washington).
wootonella Cockerell, 1909. Entomologist 42: 93. Southwestern U.S. (New Mexico).
**wyomingensis* Swenk, 1913. Univ. Stud. (Lincoln, Nebraska) 12: 52. Western U.S. (Wyoming).
xantholepis Cockerell, 1911. Proc. U.S. Natl. Mus. 41: 239. Western U.S. (Colorado).
**xanthura* Cockerell, 1908. Proc. Entomol. Soc. Washington 10: 84. Northeastern North America (New York to Nova Scotia).
?**yagensis* Tsuneki, 1973. Etizenia 66 (2): 95. Japan (northern Honshu).
?*yasha* Tsuneki, 1986. Spec. Publ. Japan Hymen. Assoc. 32: 36. Japan (Honshu).
?*yunokawana* Tsuneki, 1986. Spec. Publ. Japan Hymen. Assoc. 32: 54. Japan (northern Honshu).
ziziae Swenk, 1915. Univ. Stud. (Lincoln, Nebraska) 15: 158. North-central U.S. (North Dakota).
zonalis Schwarz, 1990. Entomofauna, Supplement 5: 5. Central Asia (Nepal).
zonata pulcherrima Stöckhert, 1941. Mitt. Münchner Entomol. Ges. 31: 1086. Southern central Europe (South Tirol, northern Italy).
zonata rubricata Stöckhert, 1941. Mitt. Münchner Entomol. Ges. 31: 1086. Southwestern and central Asia.
zonata sarmatica Stöckhert, 1941. Mitt. Münchner Entomol. Ges. 31: 1087. Southern Russia.
zonata zonata Panzer, 1798. Fauna Insectorum Germanicae, Heft 53, p.20. Central Europe, southwest to Spain.
banatica Kiss, 1915. Rovart. Lap. 22: 85.
bofillana Pérez, 1913. Bol. R. Soc. Española Hist. Nat. 13: 331.

The following species were described by Tsuneki (1986) without an indication of their affinities within *Nomada*. (When describing a new species, Tsuneki usually indicated which species he considered to be its closest relatives.) One of these species (*yasuteyamana*) is known from 3 male specimens; the rest are known from only a single female specimen each. We have not personally examined any of them, but the majority of Japanese species are in the *ruficornis* group.

?**iwakiyamana* Tsuneki, 1986. Spec. Publ. Japan Hymen. Assoc. 32: 50. Japan (north Honshu).
?**nunobensis* Tsuneki, 1986. Spec. Publ. Japan Hymen. Assoc. 32: 50. Japan (Honshu).
?**tridentata* Tsuneki, 1986. Spec. Publ. Japan Hymen. Assoc. 32: 49. Japan (north Honshu).
?*yasuteyamana* Tsuneki, 1986. Spec. Pub. Japan Hymen. Assoc.32: 54. Japan (north Honshu).

armata group

Includes *fuscicornis* group of Schwarz, 1977. Mitt. Münchner Entomol. Ges. 66: 67.

armata Herrich-Schäffer, 1839. Zeitschr. Entomol. 1: 279. Widespread in Europe, including Great Britain.
cincticornis Nylander, 1848. Notis. Sällsk. Fauna Fl. Fennica Förh. 1: 182.
compta Lepeletier, 1841. Histoire Naturelle des Insectes, Hyménoptères, v. 2, p.492.
kirbyella Stephens, 1846. Illustrations of British Entomology, Suppl., Pl. 43, Fig. 1, p. 16.
lanceolata Lepeletier, 1841. Histoire Naturelle des Insectes, Hyménoptères, v. 2, p. 493.
rostrata Lepeletier, 1841 (nec Herrich-Schäffer, 1839). Histoire Naturelle des Insectes, Hyménoptères, v. 2, p.496.
bispinosa Mocsáry, 1883. Magy. Akad. Természz. Értek. 13: 64. Southern Europe, north to Hungary.
excisa Pérez, 1890. Act. Soc. Linn. Bordeaux 44: 193.
carnifex Mocsáry, 1883. Magy. Akad. Természz. Értek. 13: 66. Southwest Europe (Spain).
lituripes Pérez, 1902. Proc.-Verb. Soc. Linn. Bordeaux 57: lxii.
tridentilabris Schwarz, 1963. Boll. Ist. Entomol. Univ. Bologna 26: 226.
corcyraea Schmiedeknecht, 1882. Apidae Europaeae 1: 219. Italy; Greece (Kerkira Island).
The spelling *corcyrea* , used by Pittioni (1952) and Schwarz (1963), is incorrect.
eos Schmiedeknecht, 1882. Apidae Europaeae 1: 233. Mediterranean region (Greece, Spain, Algeria).
fallax Pérez, 1913. Bol. R. Soc. Española. Hist. Nat. 13: 328. Mediterranean region (Spain, Sicily, Algeria).
femoralis Morawitz, 1869. Hor. Soc. Entomol. Ross. 6: 66. Widespread in Europe.
dentipes Rudow, 1879. Entomol. Nachr. 5: 211.
femoralis var. *flavopunctata* Friese, 1921. Deutsche Entomol. Zeitschr. 1920: 253.
fuscicornis Nylander, 1848. Notis. Sällsk. Fauna Fl. Fennica Förh. 1: 185. Widespread in western Palearctic.
megacephala Schenck, 1874. Berliner Entomol. Zeitschr. 18: 343.
immaculata Morawitz, 1874. Hor. Soc. Entomol. Ross. 10: 179. Southwest Asia (Russia, Afghanistan, Pakistan.
linsenmaieri Schwarz, 1974. Polskie Pismo Entomol. 44: 259. Southwest and central Europe, northwest Africa.
merceti Alfken, 1909. Deutsche Entomol. Zeitschr. 1909: 44. Southwest Europe (Spain.
mutabilis Morawitz, 1870. Hor. Soc. Entomol. Ross. 7: 328. Southern and central Europe, central Asia (Nepal).
antigana Pérez, 1895. Espèces Nouvelles de Mellifères de Barbarie, p. 31.
mutabilis var. *lucifera* Schmiedeknecht, 1882. Apidae Europaeae 1: 214.

nausicaa Schmiedeknecht, 1882. Apidae Europaeae 1: 228. Mediterranean region (Southeast Europe, Turkey, Israel).
nitida Schwarz, 1977. Mitt. Münchner Entomol. Ges. 66: 62. Northwest Africa (Algeria, Morocco).
panurgina Morawitz, 1869. Hor. Soc. Entomol. Ross. 6: 69. Southern Europe north to Switzerland; northwest Africa.
julliani Schmiedeknecht, 1882. Apidae Europaeae 1: 208.
julliani Dalla Torre, 1896. Catalogus Hymenopterorum, v. 10, p. 353. Emendation.
panurginoides Saunders, 1908. Trans. Entomol. Soc. London 2: 232. Northwest Africa.
polyacantha Pérez, 1895. Espèces Nouvelles de Mellifères de Barbarie, p. 31. North Africa (Algeria).
multispinosa Saunders, 1908. Trans. Entomol. Soc. London 2: 231.
pruinosa Pérez, 1895. Espèces Nouvelles de Mellifères de Barbarie, p. 27. North Africa (Tunisia, Morocco, Egypt).
rubricoxa Schwarz, 1977. Mitt. Münchner Entomol. Ges. 66: 64. Southwest Europe (Portugal, Spain).
rufoabdominalis Schwarz, 1963. Boll. Ist. Entomol. Univ. Bologna 26: 221. Southern Europe (Italy).
sanguinea Smith, 1854. Catalogue of Hymenopterous Insects in the Collection of the British Museum. Apidae. 2: 246. Southern France, Pyrenees, northwest Africa.
clara Pérez, 1895. Espèces Nouvelles de Mellifères de Barbarie, p. 30.
coelomeria Pérez, 1884. Act. Soc. Linn. Bordeaux 37: 367.
laevilabris Schmiedeknecht, 1882. Apidae Europaeae 1: 231.
serricornis Pérez, 1884. Act. Soc. Linn. Bordeaux 37: 370. Southern France.
sicula Schwarz, 1974. Polskie Pismo Entomol. 44: 262. Sicily.
similis Morawitz, 1872. Verh. Zool. Bot. Ges. Wien 22: 386. Widespread in western Palearctic.
nigroantennata Schmiedeknecht, 1882. Apidae Europaeae 1: 230.
?*sternalis* Pérez, 1902. Proc.-Verb. Soc. Linn. Bordeaux 57: lxii. (type lost, may be synonym of *sanguinea* Smith). North Africa (Algeria).
transitoria Schmiedeknecht, 1882. Apidae Europaeae 1: 222. Spain, southern Russia.
unispinosa Schwarz, 1981. Entomofauna 2: 376. Turkey, Italy.

"*plumosa* assemblage" (see Alexander, 1994):

felici Schwarz, 1977. Mitt. Münchner. Entomol. Ges. 66: 74. Northwest Africa (Tunisia).
hirticeps Pérez, 1895. Espèces Nouvelles de Mellifères de Barbarie, p. 32. Northwest Africa.
lamellata Schwarz, 1977. Mitt. Münchner Entomol. Ges. 66: 77. Southwest Europe (Spain, Portugal).
plumosa Gribodo, 1894. Bull. Soc. Entomol. Italiana 25: 421. Northwest Africa (Algeria).

belfragei group

Nomada subgenus *Phelonomada* Snelling, 1986. Contrib. Sci., Los Angeles Cty. Mus., 376: 24, 27, 28. Type species: *Nomada belfragei* Cresson, 1878; original designation.

belfragei Cresson, 1878. Trans. American Entomol. Soc. 7: 72. Central U.S. (Texas, Kansas).
belfragei var. *xanthogaster* Cockerell, 1911. Proc. U.S. Natl. Mus. 39: 644.
wheeleri engelmanniae Cockerell, 1911. Proc. U.S. Natl. Mus. 39: 649. South-central U.S. (Texas).
wheeleri wheeleri Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55:604. South-central U.S. (Texas)

superba group

Holonomada Robertson, 1903. Canadian Entomol. 35: 174, 177. Type species: *Nomada superba* Cresson, 1863; original designation.

affabilis affabilis Cresson, 1878. Trans. American Entomol. Soc. 7: 74. Eastern North America.
affabilis dallasensis Cockerell, 1911. Proc. U.S. Natl. Mus. 39: 654. South-central and southeastern U.S.
agrestis Fabricius, 1787. Mantissa Insectorum, v. 1, p. 306. Southern Europe, northwest Africa.
cristata Pérez, 1895. Espèces Nouvelles de Mellifères de Barbarie, p. 30. Mediterranean region (Spain, Tunisia, Morocco).
difficilis Friese, 1921. Deutsche Entomol. Zeitschr. 1920: 257. Asia Minor.
edwardsii edwardsii Cresson, 1878. Trans. American Entomol. Soc. 7: 72. Western U.S. and Canada, northwest Mexico.
intercepta Smith, 1879. Descriptions of New Species of Hymenoptera in the Collection of the British Museum, p. 100.
edwardsii var. *australior* Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 562.
edwardsii vinnula Cresson, 1879. Western U.S. (Nevada).
vinnula Cresson, 1879. Trans. American Entomol. Soc. 7: 202.
fuscipennis Lepeletier, 1841. Histoire Naturelle des Insectes, Hyménoptères, v. 2, p.474. Northwest Africa (Algeria).
grandis Cresson, 1875. Chapter 7 *In* Report of the Geographic and Geological Exploration and Survey West of the 100th Meridian, v. 5, p. 725. Western U.S. (Colorado, Texas).
magnifica Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 587.
hemphilli Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 561. Western U.S., northwestern Mexico (Baja California).
excellens Cockerell, 1903 (nec Pérez, 1913). Proc. Acad. Nat. Sci. Philadelphia 55: 573.
excurrens Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 562.
henningeri Evans, 1972. Wasmann Jour. Biol. 30: 21. Southwestern U.S. (New Mexico, Texas).
hurdi Evans, 1972. Wasmann Jour. Biol. 30: 22. Western U.S. (southern California).
imperialis Schmiedeknecht, 1882. Apidae Europaeae 1: 99. Mediterranean region (southeastern Europe, Asia Minor, Israel, Syria).
linsleyi Evans, 1972. Wasmann Jour. Biol. 30: 26. Western U.S. (California).
lucidula Schwarz, 1967. Beitr. Entomol. 17: 532. Mediterranean region (Albania, Greece, Turkey, Israel).
moravitzii Radoszkowski, 1876. Hor. Soc. Entomol. Ross. 12: 93. Southwest Asia (Caucasus).
morawitzi Radoszkowski in Dalla Torre, 1896. Catalogus Hymenopterorum, v. 10: 357. Lapsus calami or emendation?
oculata Friese, 1921. Deutsche Entomol. Zeitschr. 1920: 257. Asia Minor (Turkey).
parkeri Evans, 1972. Wasmann Jour. Biol. 30: 28. Southwestern U.S. (Arizona, New Mexico).
pecosensis Cockerell, 1903. Southwestern U.S. (New Mexico, Colorado).
xanthophila var. *pecosensis* Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 585.
pectoralis Morawitz, 1877. Hor. Soc. Entomol. Ross. 14: 103. Southern and eastern Europe.
pectoralis var. *atroflava* Friese, 1921. Deutsche Entomol. Zeitschr. 1920: 251.
pictiscutum Alfken, 1927. Konowia 6: 115. North Africa (Libya).
podagrica Gribodo, 1894. Bull. Soc. Entomol. Italiana 25: 423. Northwest Africa (Algeria, Tunisia).
quinquefasciata Schwarz, 1981. Entomofauna 2: 368. Asia Minor (Turkey).
rhodotricha Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 562. Western U.S. (California).
sexfasciata Panzer, 1799. Fauna Insectorum Germanicae, Heft 62, p. 18. Eurasia, North Africa.

connexa (Kirby), 1802. Monographia Apum Angliae, v. 2, p. 199 [*Apis*].
schaefferella (Kirby), 1802. Monographia Apum Angliae, v. 2, p. 199 [*Apis*].
?*vespoides* (Schranck), 1781. Enumeratio Insectorum Austriae Indigenorum, p. 408 [*Apis*] Nomen dubium.
superba malvastri Swenk, 1913. Univ. Stud. (Lincoln, Nebraska) 12: 80. Central U.S. (Nebraska).
nebrascensis Swenk, 1913. Univ. Stud. (Lincoln, Nebraska) 12: 80.
superba superba Cresson, 1863 (nec Pérez, 1902). Proc. Entomol. Soc. Philadelphia 2: 281. Eastern and central U.S., west to Colorado.

basalis group

?*Nomada* subgenus *Laminomada* Rodeck, 1947. Ann. Entomol. Soc. America 40: 266. Type species: *Nomada hesperia* Cockerell, 1903b; original designation (see Comments in Alexander, 1994).

basalis Herrich-Schäffer, 1839 (nec Pérez, 1895). Zeitschr. Entomol. 1: 282. Eurasia, North Africa.
andalusica Schmiedeknecht, 1882. Apidae Europaeae 1: 124.
astarte Pérez, 1895. Espèces Nouvelles de Mellifères de Barbarie, p. 29.
bimaculata Eversmann, 1852 (nec Schilling, 1849). Bull. Soc. Imp. Nat. Moscou 25: 99.
emendata Schulz, 1906. Spolia Hymenopterologica, p. 259. Nomen novum for *rubra* Smith, 1849 (nec Geoffrey, 1785; nec Eversmann, 1852; nec Provancher, 1888).
flavomaculata Lucas, 1849. Exploration Scientifique de l'Algerie, Zoologie, v. 3, p. 216.
flavomaculata var. *carnea* Friese, 1921. Deutsche Entomol. Zeitschr. 1920: 253.
grossa Friese, 1921. Deutsche Entomol. Zeitschr. 1920: 258.
regalis Morawitz, 1870. Hor. Soc. Entomol. Ross. 7: 332.
regalis var. *inderskiana* Lozinski, 1922. Bull. Int. Acad. Polonaise Sci. Let. Cl. Sci. Math. Nat. Ser. B 1921: 110.
rubra Smith, 1849. Zoologist 7: App. p. xli.
tricolor Brullé, 1832. Expédition Scientifique de Morée, Zoologie, 3(2):345. Nomen oblitum (see Schwarz, 1986).
tripunctata Morawitz, 1872. Hor. Soc. Entomol. Ross. 8: 229.
cherkesiana Mavromoustakis, 1955. Ann. Mag. Nat. Hist. (12)8: 102. Cyprus.
dubia Eversmann, 1852 (nec Schmiedeknecht, 1882). Bull. Soc. Imp. Nat. Moscou 25: 94. Western Asia (Russia).
?*flavinervis* Brullé, 1832. Expédition Scientifique de Morée, Zoologie. 3 (2): 344. Greece.
?*flavozonata* Nurse, 1902. Jour. Asia. Soc. Bengal 70: 148. Northern India (Punjab).
?*hesperia falconis* Rodeck, 1947. Ann. Entomol. Soc. America 40: 270. Western U.S. (California).
?*hesperia hesperia* Cockerell, 1903. Proc. Acad. Nat. Sci. Philadelphia 55: 563. Western U.S. (California, Oregon, Washington).
flavopicta Swenk, 1913 (nec Kirby, 1802). Univ. Stud. (Lincoln, Nebraska) 12: 84.
incisa Schmiedeknecht, 1882. Apidae Europaeae 1: 101. Southeastern Europe.
insignipes insignipes Schmiedeknecht, 1882. Apidae Europaeae 1: 128. Southern Europe.
insignipes leucosticta Pérez, 1884. Southern Europe (France, Sicily).
leucosticta Pérez, 1884. Act. Soc. Linn. Bordeaux 37: 337.
japonica Smith, 1873. Trans. Entomol. Soc. London: 203. Eastern Asia (throughout Japan, Ryukyu Islands, Korea, China.
daimio Matsumura, 1912. Thousand Insects of Japan, Suppl. 4: 197.
versicolor Smith, 1854. Catalogue of the Hymenoptera in the Collection of the British Museum, v. 2, p. 242. Preoccupied.
xanthidica Cockerell, 1905. Trans. American Entomol. Soc. 31: 313. Nomen novum for *versicolor* Smith, 1854 (nec Panzer, 1798).
keroanensis Pérez, 1895. Espèces Nouvelles de Mellifères de Barbarie, p. 27. Northwest Africa.
lateritia Mocsáry, 1883. Magy. Akad. Termész. Értek. 13: 63. Asia Minor (Turkey, Iran).
limassolica Mavromoustakis, 1955. Mediterranean region (Cyprus).
flavinervis var. *limassolica* Mavromoustakis, 1955. Ann. Mag. Nat. Hist. (12)8: 99.
mocsaryi Schmiedeknecht, 1882. Apidae Europaeae 1: 133. Southeastern Europe, Asia Minor.
nesiotica Mavromoustakis, 1958. Ann. Mag. Nat. Hist. (12)10: 845. Mediterranean region (Cyprus).
nobilis Herrich-Schäffer, 1839. Zeitschr. Entomol. 1: 287. Southern Europe, Asia Minor east to Iran.
aberrans Eversmann, 1852. Bull. Soc. Imp. Nat. Moscou 25: 93.
calabra Morawitz, 1872. Hor. Soc. Entomol. Ross. 8: 230.
nobilis var. *magrettiana* Schmiedeknecht, 1882. Apidae Europaeae 1: 86.
pesenkoi Schwarz, 1987. Entomofauna 8: 464. Southwest Asia (Tadzhikistan, Turkmenistan).
?*regina* Friese, 1921. Deutsche Entomol. Zeitschr. 1920: 256. Spain.
?*samarcandica* Friese, 1921. Deutsche Entomol. Zeitschr. 1920: 255. Turkestan.
subvirescens Morawitz, 1875. Izv. Imp. Obshch. Ljubrit. Estest. Antrop. Etnogr. 19(2): 149. Southwestern Asia (Turkestan).
desertorum Morawitz, 1875. Izv. Imp. Obshch. Ljubrit. Estest. Antrop. Etnogr. 19(2): 152.
sybarita Schmiedeknecht, 1882. Apidae Europaeae 1: 134. Eastern Europe (Hungary).

bifasciata group

accentifera Pérez, 1895. Espèces Nouvelles de Mellifères de Barbarie, p. 28. Northwest Africa.
bifasciata bifasciata Olivier, 1811. Encyclopédie Méthodique. Dictionnaire des Insectes, v. 8, p. 365. Mediterranean region.
planiscuta Saunders, 1908. Trans. Entomol. Soc. London 2: 229.
pusilla Pérez, 1884. Act. Soc. Linn. Bordeaux 37: 330 et pl. auctt., (nec Rossi, 1792; nec Lepeletier, 1841; see Schwarz, 1986).
bifasciata lepeletieri Pérez, 1884. Southern and central Europe.
lepeletieri Pérez, 1884. Act. Soc. Linn. Bordeaux 37: 330.
navasi Dusmet, 1913: Mem. R. Soc. Española Hist. Nat. 9: 259.
comparata Cockerell, 1911. Japan (Hokkaido, Honshu).
maculifrons var. *comparata* Cockerell, 1911. Proc. U.S. Natl. Mus. 39: 644.
duplex Smith, 1854. Catalogue of the Hymenoptera in the Collection of the British Museum, v. 2, p. 244. Southwest Europe, northwest Africa.
cirtana Pérez, 1895. Espèces Nouvelles de Mellifères de Barbarie, p. 28.
fucata melanoscapa Gribodo, 1894. Bull. Soc. Entomol. Italiana 26: 79.
fucata nigroflavida Gribodo, 1894. Bull. Soc. Entomol. Italiana 26: 79.
sardiniensis Friese, 1921. Deutsche Entomol. Zeitschr. 1920: 261.
?*ferghanica* Morawitz, 1875. Izv. Imp. Obshch. Ljubrit. Estest. Antrop. Etnogr. 19(2): 148. Central Asia (Turkestan).
scutellaris Morawitz, 1895 (nec Olivier, 1811). Hor. Soc. Entomol. Ross. 29: 54.
fucata fucata Panzer, 1798. Fauna Insectorum Germanicae, Heft 55, p. 19. Eurasia, North Africa.
fucata var. *caucasica* Lozinski, 1922. Bull. Int. Acad. Polonaise Sci. Let. Cl. Sci. Math. Nat. Ser. B. 1921: 103.
fucata var. *flavescens* Friese, 1921 (nec *pampicola* var. *flavescens* Friese, 1916). Deutsche Entomol. Zeitschr. 1920: 254.

fucata var. *iberica* Dalla Torre & Friese, 1894. Entomol. Nachr. 20: 39.
fucata var. *pretiosa* Friese, 1921. Deutsche Entomol. Zeitschr. 1920: 253.
fucata var. *taeniata* Gribodo, 1894. Bull. Soc. Entomol. Italiana 26: 79.
varia Panzer, 1798. Fauna Insectorum Germanicae, Heft 55, p.20.
?*ginran* Tsuneki, 1973. Etizenia 66(2): 85. Japan (Hokkaido, Honshu, Kyushu)
harimensis Cockerell, 1914. Ann. Mag. Nat. Hist. (8)13: 426 (female, not male).
goodeniana (Kirby) 1802. Monographia Apum Angliae, v. 2, p. 180. Northern and central Europe, east to Turkestan and Siberia [*Apis*].
alternata (Kirby), 1802. Monographia Apum Angliae, v. 2, p. 182 [*Apis*].
batava Vollenhoven, 1858. Herklots Bouwstoffen II. P.3, p. 283.
cincta Herrich-Schäffer, 1839 (nec Rossi, 1792; nec Lepeletier, 1841). Zeitschr. Entomol. 1: 288.
goodeniana ssp.*danuvia* Pittioni, 1951. Entomol. Nachrichtenbl. Österr. Schweizer Entom. 3: 155.
integra Imhoff, 1834 (nec Brullé, 1832; nec Robertson, 1893). Isis 1834: 374.
scheviakovi Cockerell, 1928. Ann. Mag. Nat. Hist. (10)1: 349.
succincta var. *lineolata* Friese, 1921. Deutsche Entomol. Zeitschr. 1920: 254.
illustris Schmiedeknecht, 1882. Apidae Europaeae 1: 104. Italy.
dusmetella Pérez, 1913. Bol. R. Soc. Española Hist. Nat. 13: 331.
mauritanica mauritanica Lepeletier, 1841. Histoire Naturelle des Insectes, Hyménoptères, v. 2, p. 464. Southern Europe, northwest Africa.
lynesi Cockerell, 1933. Entomologist 66: 242.
mephisto Schmiedeknecht, 1882. Apidae Europaeae 1: 117.
numida Lepeletier, 1841. Histoire Naturelle des Insectes, Hyménoptères, v. 2, p. 465.
poecilonota Pérez, 1895. Espèces Nouvelles de Mellifères de Barbarie, p. 28.
poultoni Saunders, 1901. Entomol. Mon. Mag. 37: 209.
mauritanica manni Morawitz, 1872. Mediterranean region (southern Europe, Algeria).
manni Morawitz, 1872. Hor. Soc. Entomol. Ross. 8: 227.
melanopyga Schmiedeknecht, 1882. Apidae Europaeae 1: 139. Southeast Europe.
?**pekingensis* Tsuneki, 1986. Spec. Publ. Japan Hymen. Assoc. 32: 32. Northeastern China (Peking).
?*scutellata* Friese, 1921. Deutsche Entomol. Zeitschr. 1920: 262. Spain.
?*siciliensis* Dalla-Torre & Friese, 1894. Entomol. Nachr. 20: 42. Sicily. Nomen novum for *parvula* De Stefani, 1885.
parvula De Stefani, 1885 (nec Lucas, 1846; nec Holmberg, 1886). Nat. Siciliana 4: 189. Preoccupied.
succincta Panzer, 1798. Fauna Insectorum Germanicae, Heft 55, p.21. Widespread in Europe.
fulvicornis auctt. (nec Fabricius,1793).
succincta var. *mixta* Dalla Torre, 1877. Zeitschr. Ferdinandeum Innsbruck (3)21: 165.
sexfasciata var. *mixta* in Dalla Torre, 1896. Catalogus Hymenopterorum, v. 10, p. 368. Lapsus.
?*succincta* var. *rufula* Friese, 1921. Deutsche Entomol. Zeitschr. 1920: 254.

trispinosa group

?*babai* Tsuneki, 1986. Spec. Publ. Japan Hymen. Assoc. 32: 36. Japan (Honshu).
brevis Saunders, 1908. Trans. Entomol. Soc. London 2: 230. Northwest Africa (Algeria).
meyeri Dusmet, 1932. Eos 8: 226.
hera Schwarz, 1965. Nachr. Bayerischen Entomol. 14: 81. Greece.
kocoureki Schwarz, 1987. Entomofauna 8: 459. Southwest Asia (Uzbekistan).
nipponica Yasumatsu & Hirashima, 1951. Trans. Shikoku Entomol. Soc. 2: 53. Korea, Japan (Hokkaido, Honshu, Kyushu).
polemediana Mavromoustakis, 1957. Beitr. Entomol. 7: 47. Mediterranean region (Cyprus).
trispinosa trispinosa Schmiedeknecht, 1882. Apidae Europaeae 1: 121. Southeast Europe, north to Austria; Asia, east to northeast China.
trispinosa cypria Mavromoustakis, 1952. Mediterranean region (Cyprus).
trispinosa var. *cypria* Mavromoustakis, 1952. Ann. Mag. Nat. Hist. (12)5: 842.
?*xanthopoda* Schwarz, 1990. Entomofauna, Supplement 5: 11. Afghanistan, Pakistan.

furva group

Includes *furva* group of Stöckhert, 1943. Deutsche Entomol. Zeitschr. 1943: 89-126.

adusta Smith, 1875. Trans. Entomol. Soc. London: 50. Asia (Nepal, India, Burma).
?*anpingensis* Strand, 1913. Suppl. Entomol. Berlin, No. 2: 53. Asia (Taiwan).
antennata Meade-Waldo, 1913. Ann. Mag. Nat. Hist. (8)12: 100. Asia (Sri Lanka).
?*atrocincta* Friese, 1920. Deutsche Entomol. Zeitschr. 1920: 263. Asia (Taiwan).
attenuata Cockerell, 1929. Ann. Mag. Nat. Hist. (10)4: 18. Asia (Thailand).
attrita Cockerell, 1919. Philippine Jour. Sci. 14: 84. Asia (Philippines).
australensis Perkins, 1912. Ann. Mag. Nat. Hist. (8)9: 116. Australia (Queensland).
bakeri Cockerell, 1915. Ann. Mag. Nat. Hist. (8)15: 263. Asia (Philippines).
banahaonis Cockerell, 1915. Ann. Mag. Nat. Hist. (8)15: 264. Asia (Philippines).
bicellula Schwarz, 1990. Entomofauna, Supplement 5: 40. Asia (Pakistan, India, Sri Lanka).
biguttata Friese, 1909. Ann. Hist. Nat. Mus. Natl. Hungary 7: 259. New Guinea.
?*biroi* Friese, 1909. Ann. Hist. Nat. Mus. Natl. Hungary 7: 259. New Guinea.
?*biroi* var. *nigrescens* Friese, 1909. Ann. Hist. Nat. Mus. Natl. Hungary 7: 259. New Guinea.
blepharipes Schmiedeknecht, 1882. Apidae Europaeae 1: 127. Southern Europe, north to Switzerland and Hungary.
helvetica Schmiedeknecht, 1882. Apidae Europaeae 1: 225.
erythrocephala auctt. nec Morawitz, 1871.
bluethgeni Stöckhert, 1943. Deutsche Entomol. Zeitschr. 1943: 95, 102, 121. Central and southeast Europe. Emendation according to ICZN, Article 32d.i(3).
blüthgeni Stöckhert, 1943. Deutsche Entomol. Zeitschr. 1943: 121.
bouceki Kocourek, 1985. Entomofauna 6: 189. Europe (Czechoslavakia).
breviuscula Schwarz, 1990. Entomofauna, Supplement 5: 32. Asia (India).
ceylonica Cameron, 1897. Mem. Manchester Lit. Phil. Soc. 41(4): 123. Asia (Sri Lanka).
collarae Schwarz, 1964. Polskie Pismo Entomol. 34: 55. Asia (Iraq).
concessa Cockerell, 1919. Philippine Jour. Sci. 14: 84. Asia (Philippines).
connectens Pérez, 1884. Act. Soc. Linn. Bordeaux 37: 364. Europe (Southern France, Sicily).
conspicua Smith, 1863. Proc. Linn. Soc. London Zool. 7: 47. Timor.

cordilabris Schwarz, 1990. Entomofauna, Supplement 5: 39. Asia (India).
coronata Pérez, 1895. Espèces Nouvelles de Mellifères de Barbarie, p. 28. Mediterranean region (Spain, Algeria, Tunisia).
curvispinosa Schwarz, 1981. Entomofauna 2: 407. Mediterranean region (Turkey, Israel).
cypricola Mavromoustakis, 1957. Ann. Mag. Nat. Hist. (12)10: 333. Mediterranean region (Cyprus).
?*dahli* Friese, 1912. Mitt. Zool. Mus. Berlin 6: 95. Bismark Archipelago.
diacantha Schwarz, 1981. Entomofauna 2: 401. Mediterranean region (Greece, Bulgaria, Turkey, Syria).
discedens Pérez, 1884. Act. Soc. Linn. Bordeaux 37: 361. Europe (Southern France).
dissessa Cockerell, 1920. Philippine Jour. Sci. 17: 622. Asia (Philippines).
distinguenda Morawitz, 1874. Hor. Soc. Entomol. Ross. 10: 181. Northwest Africa to Afghanistan.
rugithorax Pérez, 1902. Proc.-Verb. Soc. Linn. Bordeaux 57: lix.
erythrocephala Morawitz, 1870. Hor. Soc. Entomol. Ross. 7: 331. Southern Europe, north to Hungary and Switzerland.
exheredans Cockerell, 1919. Philippine Jour. Sci. 14: 84. Asia (Philippines).
furva furva Panzer, 1798. Fauna Insectorum Germanicae, Heft 55, p.23. Central and southern Europe.
?*furva nigricans* Schmiedeknecht, 1882. Southern Europe, northwest Africa.
furva var. *nigricans* Pérez. *In* Schmiedeknecht, 1882. Apidae Europaeae 1: 199.
furvoides Stöckhert, 1944. Deutsche Entomol. Zeitschr. 1943: 119. Central Europe (central Danube region).
glaucopis Pérez, 1890. Act. Soc. Linn. Bordeaux 44: 194. Southern France, Spain, Canary Islands.
ferroviaria Dusmet, 1913. Mem. R. Soc. Española Hist. Nat. 9: 34.
?*pusilla* Lepeletier, 1841 (nec Rossi, 1792). Histoire Naturelle des Insectes, Hyménoptères, v. 2., p. 466. Algeria. Preoccupied. (Type apparently lost, see Schwarz, 1986.)
?*grandior* Friese, 1921. Deutsche Entomol. Zeitschr. 1920: 254. Northwest Africa (Algeria).
furva var. *grandior* Friese, 1921. Deutsche Entomol. Zeitschr. 1920: 254.
guichardi Schwarz, 1981. Entomofauna 2: 371. Mediterranean region (Turkey, Israel).
gusenleitneri Schwarz, 1981. Entomofauna 2: 395. Mediterranean region (Turkey).
?*hirtiventris* Schwarz, 1990. Entomofauna, Supplement 5: 48. Asia (Nepal).
insularis Smith, 1863. Proc. Linn. Soc. London Zool. 7: 47. Seram.
?*javanica* Friese, 1909. Ann. Hist. Nat. Mus. Natl. Hungary 7: 260. Java.
kohli Schmiedeknecht, 1882. Apidae Europaeae 1: 203. Central Europe, northwest Africa.
hipponensis Saunders, 1908. Trans. Entomol. Soc. London 2: 234.
laticrus Mocsáry, 1883. Magy. Akad. Termész. Értek 13: 66. Asia Minor.
erythrosoma Mocsáry, 1883. Magy. Akad. Termész. Értek. 13: 68.
?*leucotricha* Strand, 1914. Arch. Naturg. 80A: 141. Taiwan.
?*longicornis* Friese, 1920. Deutsche Entomol. Zeitschr. 1920: 263. Taiwan.
lucilla Nurse, 1902. Jour. Asia. Soc. Bengal 70: 149. India.
lusca Smith, 1854. Catalogue of the Hymenoptera in the Collection of the British Museum, v. 2, p. 243. India, Sri Lanka, Burma, Philippines.
makilingensis Cockerell, 1915. Ann. Mag. Nat. Hist. (8)15: 263. Philippines.
malayana Cameron, 1909. Entomologist 42: 16. Borneo.
mindanaonis Cockerell, 1915. Ann. Mag. Nat. Hist. (8)15: 263. Philippines.
?*monozona* Friese, 1920. Deutsche Entomol. Zeitschr. 1920: 264. Taiwan.
?*nepalensis* Schwarz, 1990. Entomofauna, Supplement 5: 52. Nepal.
nigrovaria Pérez, 1895. Espèces Nouvelles de Mellifères de Barbarie, p. 28. Northwest Africa.
gerundica Pérez, 1913. Bol. R. Soc. Española. Hist. Nat. 13: 330.
oralis Schwarz, 1981. Entomofauna 2: 411. Turkey.
orbitalis Pérez, 1913. Bol. R. Soc. Española Hist. Nat. 13: 325. Spain, France.
ovaliceps Schwarz, 1981. Entomofauna 2: 385. Turkey, Israel.
palavanica Cockerell, 1919. Philippine Jour. Sci. 14: 84. Philippines (Palawan).
papuana Cockerell, 1933. Stylops 2: 42. New Guinea.
penangensis Cockerell, 1920. Ann. Mag. Nat. Hist. (9)5: 118. Malaya (Penang Island).
pervasor Cockerell, 1919. Philippine Jour. Sci. 14: 84. Philippines.
picticauda Cockerell, 1929. Ann. Mag. Nat. Hist. (10)4: 147. Malaya.
polyodonta Cockerell, 1920. Philippine Jour. Sci. 17: 622. Malaya (Penang Island).
?*posthuma* Blüthgen, 1949. Beitr. Tax. Zool. 1: 83. Eastern Europe (Poland), Nepal.
mixtella Noskiewicz, 1959. Polskie Pismo Entomol. 29: 131.
priesneri Schwarz, 1965. Nachr. Bayerischen Entomol. 14: 84. Crete.
priscilla Nurse, 1902. Jour. Asia. Soc. Bengal 70: 150. Pakistan, India, Sri Lanka.
psilocera Kohl, 1908. Denkschr. K. Akad. Wiss. Math.-Nat. Kl. (Wien) 81: 308. Solomon Islands.
pulawskii Tsuneki, 1973. Etizenia 66(2): 125. Japan (Honshu).
?*rhinula* Strand, 1914. Arch. Naturg. 80A: 142. Taiwan.
sandacana Cockerell, 1920. Philippine Jour. Sci. 17: 223. Borneo.
?*secessa* Cockerell, 1911. Ann. Mag. Nat. Hist. (8)7: 230. Taiwan.
sheppardana minuscula Noskiewicz, 1930. Central Europe.
minuscula Noskiewicz, 1930. Polskie Pismo Entomol. 9: 260.
microsticta Cockerell, 1931. Ann. Mag. Nat. Hist. (10)8: 412.
sheppardana okubira Tsuneki, 1973. Etizenia 66(2): 122. Japan.
sheppardana sheppardana (Kirby) 1802. Monographia Apum Angliae, v. 2, p. 217 [*Apis*]. Northern and central Europe.
dalii Curtis, 1832. British Entomology, v. 9, pl. 419.
[*Dahlii* Curtis 1832 in Dalla Torre, 1896. Cat. Hym. 10: 349 is an incorrect spelling]
?*smyrnaensis* Friese, 1920. Deutsche Entomol. Zeitschr. 1920: 262. Turkey (Smyrna).
subpetiolata Smith, 1879. Descriptions of New Species of Hymenoptera in the Collections of the British Museum, p.99. Borneo.
sutepensis Cockerell, 1929. Ann. Mag. Nat. Hist. (10)4: 147. Thailand.
taicho Tsuneki, 1973. Etizenia 66 (1): 47. Japan (Honshu).
testaceobalteata Cameron, 1910. Entomologist 43: 7. Borneo.
turneri Meade-Waldo, 1913. Ann. Mag. Nat. Hist. (8)12: 98. India, Nepal.
wickwari Meade-Waldo, 1913. Ann. Mag. Nat. Hist. (8)12: 99. Sri Lanka.
yarrowi Schwarz, 1981. Entomofauna 2: 389. Turkey.

Nomada species incertae sedis

Most of these are published names for which the type has been lost or may have never existed (e.g. names attributed to Scopoli, Rossi, Olivier). Other names, such as those attributed to Morawitz, Mocsáry, or Dusmet, may be resolved in the future, but we have not seen the types, and they are not among the names attributed to these authors upon which later revisers have so far published. Illiger (1806) proposed 28 new species names that are listed in Dalla Torre's (1896) catalog with the parenthetical note "s. descr.".

According to the International Code of Zoological Nomenclature (Article 12), these names are not available because they are not accompanied by a description, definition, or indication. Although Illiger refers to a collection that contains specimens upon which his names are based, Article 12c of the code stipulates that mention of a specimen "does not in itself constitute a description, definition, or indication". Consequently, we are treating Illiger's names as nomina nuda, and they are not included in the following list.

annularis Olivier, 1811. Encyclopédie Méthodique. Dictionnaire des Insectes, v. 8, p. 366. Southern France.
arenaria Panzer, 1804. System. Nomencl., p. 197. Germany.
baldiniana Benzi, 1892. Atti Soc. Nat. Modena (3)11: 220. Italy.
bimaculata Schilling, 1849. Arbeit. Schles. Ges. Vaterl. Kultur 1848: 103. Poland (Silesia).
bipunctata Fabricius, 1805. Systema Piezatorum, p. 392. Asia (Tranquebar).
brunnea Schilling, 1849. Arbeit. Schles. Ges. Vaterl. Kultur 1848: 103. Poland (Silesia).
cincta Rossi, 1792. Mantissa Insectorum, p. 146. Italy.
dolosa Mocsáry, 1883. Magy. Akad. Termész. Értek 13: 67. Spain.
ferruginea Olivier, 1811. Encyclopédie Méthodique. Dictionnaire des Insectes, v. 8, p. 370. Syria.
flavicornis Rossi, 1790. Fauna Etrusca, v. 2, p. 112. Italy.
fulvipes Brullé, 1832. Expédition Scientifique de Morée, Zoologie, v. 2, p. 344. Southern Europe (Greece). (type apparently lost.)
guilochei Dusmet, 1915. Mem. R. Soc. Española Hist. Nat. 8 (Mem. 7): 331.
hananoi Yasumatsu & Hirashima, 1952. Kontvu 19: 84. Southern Manchuria.
integricollis Morawitz, 1894. Hor. Soc. Entomol. Ross. 28: 60. Southwestern Asia (Turkestan).
interrupta Panzer, 1798 (nec Fowler, 1899). Fauna Insectorum Germanicae, v. 53, Heft 53, p. 24.
jacobaeae Panzer, 1799. Fauna Insectorum Germanicae (72): 20. Nomen dubium.
jaramensis Dusmet, 1913. Mem. R. Soc. Española Hist. Nat. 9: 310. Spain.
kirbyi Lepeletier, 1841. Histoire Naturelle des Insectes, Hyménoptères, v. 2, p. 485. Algeria.
krueperi Schmiedeknecht, 1882. Southern Europe (Greece). Emendation according to ICZN, Article 32d.i(3).
krüperi Schmiedeknecht, 1882. Apidae Europaeae 1: 232 [type apparently lost].
kurilensis Yasumatsu, 1939. Trans. Kansai Entomol. Soc. 9: 6. Kurile Islands.
labiata Olivier, 1811. Encyclopédie Méthodique. Dictionnaire des Insectes, v. 8, p. 368. France.
lebanensis Mavromoustakis, 1959. Entomol. Bericht. 19: 31. Lebanon.
melanostoma Herrich-Schäffer, 1839. Zeitschr. Entomol. 1: 280. Nomen dubium.
melitensis Costa, 1893. Atti Accad. Sci. Fis. Mat. Napoli Vol. 5, Ser. 2, No. 14:. 28. Malta.
morio (Swederus) 1787. Svensk. Vet-Akad. Handl. 8: 283. South America (Brazil) [*Apis*].
nasuta Scopoli, 1770. Annus Historico Naturalis, v. 4:, p. 47. Italy (Carnia).
nigella Nylander, 1848. Notis. Sällsk. Fauna Fl. Fennica Förh. 1 (Adn.): 176. Europe; Asia (Siberia).
nigricollis Morawitz, 1875. Izv. Imp. Obshch. Ljubrit. Estest. Antrop. Etnogr. 19(2): 158. Southwest Asia (Tashkent).
nigropalliata Hedicke, 1938. Sitzungsber. Ges. Naturf. Fr. Berlin 1938: 123. Palestine.
nigrorufa Retzius, 1783. Caroli De Geer Genera et Species Insectorum..., p. 62.
obliqua Olivier, 1811 (nec Fowler, 1899). Encyclopédie Méthodique. Dictionnaire des Insectes, v. 8, p. 366. France.
ornata Eversmann, 1852. Bull. Soc. Imp. Nat. Moscou 25: 98. European Russia.
pallescens Herrich-Schäffer, 1839. Zeitschr. Entomol. 1: 281. Nomen dubium; treated by Pittioni (1952, p. 273) as synonym of *alboguttata alboguttata* Herrich-Schäffer, but original description corresponds more closely to *striata* Fabricius.
parvula Lucas, 1849. Exploration Scientifique de l'Algerie, Zoologie, v. 3, p. 215. Northwest Africa (Algeria).
perezi Dusmet, 1913. Mem. R. Soc. Española Hist. Nat. 9: 357. Spain.
persica Dusmet, 1915. Trab. Mus. Nac. Cienc. Nat., Ser. Zool. 22: 6.
planifrons Lozinski, 1922. Bull. Int. Acad. Polonaise Sci. Let. Cl. Sci. Math. Nat. Ser. B 1921: 116. Eastern Siberia.
punctata Lepeletier, 1841 (nec Smith, 1854). Histoire Naturelle des Insectes, Hyménoptères, v. 2, p. 478. Algeria.
pusilla Rossi, 1792 (nec Lepeletier, 1841). Mantissa Insectorum, p. 146. Europe (Italy). (type lost?—see Schwarz, 1986, Entomofauna 7: 425).
quadrispinosa Mocsáry, 1901. Zichy Ergebn. 2: 168. Russia.
ranunculi Scopoli, 1770. Annus Historico Naturalis, v. 4, p. 46. Europe.
rufa Rossi, 1790. Fauna Etrusca, v. 2, p. 111. Italy.
rufescens Scopoli, 1770. Annus Historico Naturalis, v. 4, p. 45. Slovenia (Carnia). Type lost.
ruficeps Lepeletier, 1841. Histoire Naturelle des Insectes, Hyménoptères, v. 2, p. 475. Algeria.
ruficornis Scopoli, 1770 (nec Linnaeus, 1758). Annus Historico Naturalis, v. 4, p. 46. Type lost, Nomen dubium.
rufiventris Spinola, 1806. Insectorum Liguriae, v. 1, p. 47.
rufinasutina Strand, 1910. Entomol. Zeitschr. Stuttgart 24: 216. Algeria.
rufohirta Morawitz, 1895. Hor. Soc. Entomol. Ross. 29: 53. Southwest Asia (Turkmenistan.).
rufosoma Strand, 1921. Arch. Naturg. 87A: 301. Egypt.
schaefferi Dufour, 1841. Mém. Math. Savants Érangers 7: 422. France?
scutellaris Olivier, 1811. Encyclopédie Méthodique. Dictionnaire des Insectes, v. 8, p. 365. France.
sericea Dufour, 1841. Mém. Math. Savants Érangers 7: 422. France?
squalida Scopoli, 1770. Annus Historico Naturalis, v. 4, p. 45. Type lost, nomen dubium. Slovenia (Carnia).
subfasciata Schilling, 1827. Arbeit. Schles. Ges. Vaterl. Kultur 1826: 23. Poland (Silesia).
succincta Scopoli, 1770 (nec Panzer, 1798). Annus Historico Naturalis, v. 4, p. 45. Type lost, Nomen dubium.
sulphuripes Morawitz, 1875. Izv. Imp. Obshch. Ljubrit. Estest. Antrop. Etnogr. 19(2): 150. Southwest Asia (Uzbekistan, Samarkand).
syriaca Dusmet, 1915 (nec Friese, 1921). Trab. Mus. Nat. Cien. Nat., Ser. Zool. 22: 8. Syria.
talyschiensis Morawitz, 1886. Hor. Soc. Entomol. Ross. 20: 78. Southwest Asia (Turkestan).
terminalis Imhoff, 1834. Isis 1834: 376. Switzerland.
thoracica Morawitz, 1880. Bull. Acad. Imp. Sci. St. Petersbourg 26: 369. Eastern Asia (Mongolia).
tigridis Morice, 1921. Jour. Bombay Nat. Hist. Soc. 28: 193. Iraq.
tranquebarorum (Swederus), 1787. Svensk. Vet-Akad. Handl. 8: 282 [*Apis*]. Asia (Tranquebar).
tuberculata Lepeletier, 1841. Histoire Naturelle des Insectes, Hyménoptères, v. 2, p. 483. France.
tunetana Dusmet, 1932. Eos 8: 231. North Africa.
unifasciata Schilling, 1826. Arbeit. Schles. Ges. Vaterl. Kultur 1826: 23. Poland (Silesia).
vagans Radoszkowski, 1876. Hor. Soc. Entomol. Ross. 12: 122. Egypt.
variabilis Lucas, 1849. Exploration Scientifique de l'Algerie, Zoologie, v. 3, p. 216. Algeria.
versicolor Panzer, 1798. Fauna Insectorum Germanicae (53): 22.
zichyana Mocsáry, 1901. Zichy Ergebn. 2: 169. Russia.

LITERATURE CITED

Alexander, B.A. 1994. Species-groups and cladistic analysis of the cleptoparasitic bee genus *Nomada* (Hymenoptera: Apoidea). Univ. Kansas Sci. Bull. 55: 175-238.

Cameron, P. 1902. Descriptions of new genera and species of Hymenoptera collected by Major C.G. Nurse at Deesa, Simla, and Ferozepore. Jour. Bombay Nat. Hist. Soc. 14: 419-420.

Cockerell, T.D. A. 1926. Some bees in the collection of the California Academy of Sciences. Pan-Pac. Entomol. 3: 80-90.

Cockerell, T.D.A. 1931. The bees of Australia. Australian Zool. 7: 34-54.

Dalla Torre, C.G. 1896. Catalogus Hymenopterorum, Vol. X. Apidae (Anthophila). Lipsiae.

Dusmet y Alonso, J.M. 1915. Algunos apidos nuevos o interesantes del Museo de Madrid. Trab. Mus. Nac. Cien. Nat. (Madrid), Ser. Zool. 22: 1-18.

Eardley, C., and M. Schwarz. 1991. The Afrotropical species of *Nomada* Scopoli (Hymenoptera: Anthophoridae). Phytophylactica 23: 17-27.

Eversmann, E. 1852. Fauna Hymenopterologica Volgo-Uralensis (continuatio). Bull. Soc. Imp. Nat. Moscou 25: 1-137.

Friese, H. 1920. Neue Arten der Schmarotzerbienen. Deutsche Entomol. Zeitschr. 1921: 251-266.

Friese, H. and A. von Schulthess. 1923. Neue Hymenopteren aus palaearktisch Afrika und Asien. Konowia 2: 279-294.

Illiger, K. 1806. William Kirby's Familien der bienenartigen Insekten mit Zusätzen, Nachweisungen und Bemerkungen. Magazin für Insektenkunde 5: 28-175.

Mavromoustakis, G.A. 1955. On the bees of Cyprus. Part 6. Ann. Mag. Nat. Hist. (12)8: 97-105.

Mavromoustakis, G.A. 1957. On the bees of Cyprus. Part 7. Ann. Mag. Nat. Hist. (12)10: 321-337.

Pittioni, B. 1952. Die *Nomada*-Arten der Alten Welt: Bestimmungstabelle der Mannchen. Ann. Naturh. Mus. Wien 59: 221-291.

Schilling, P.S. 1849. Die sogenannten Einsiedler-Bienen Schlesiens. Arbeit. Schles. Ges. Vaterl. Kultur 1849: 98-104.

Schwarz, M. 1986. Zur Klärung der Nomenklatur und Synonymie der *Nomada pusilla* Lepeletier, 1841 (Hymenoptera, Apoidea). Entomofauna 7: 425-430.

Tsuneki, K. 1986. New species and subspecies of the aculeate Hymenoptera from east Asia, with some synonyms, specific remarks and distributional data. Special Publ. JapanHymen. Assoc., No. 32. pp. 1-60.

ALPHABETICAL INDEX OF NAMES AT AND BELOW THE RANK OF SPECIES

aberrans Eversmann [synonym of *nobilis* Herrich-Schäffer] 255
abnormis Ducke [*vegana* group?] 241
abtana Tsuneki [*ruficornis* group?] 244
abyssinica Meade-Waldo [*roberjeotiana* group] 242
accentifera Pérez [*bifasciata* group] 255
accepta Cresson [*ruficornis* group] 244
acutilabris Schwarz [*ruficornis* group] 244
adducta Cresson [*adducta* group] 241
adusta Smith [*furva* group] 256
advena Smith [*vegana* group] 241
aestivalis Friese [synonym of *fabriciana* Linnaeus] 247
affabilis Cresson [*superba* group] 254
affinis Dusmet [synonym of *fenestrata fenestrata* Lepeletier] 247
affinis Herrich-Schäffer [see *panzeri panzeri* Lepeletier] 251
africana Friese [*roberjeotiana* group] 242
agrestis Fabricius [*superba* group] 254
agynia Cockerell [*ruficornis* group] 244
aino Tsuneki [subspecies of *roberjeotiana* Panzer] 243
albidemaculata Lozinski [*roberjeotiana* group?] 242
albofasciata Smith [synonym of *bella bella* Cresson] 245
alboguttata Herrich-Schäffer [*ruficornis* group] 244
albopicta Morawitz [subspecies of *flavopicta* (Kirby)] 247
alboscutellata Schwarz [*ruficornis* group] 244
aldrichi Cockerell [*ruficornis* group] 244
alfkeni Cockerell [synonym of *flavoguttata flavoguttata* (Kirby)] 247
alfkeni Gaunitz [synonym of *obscura* Zetterstedt] 250
alfkeni Noskiewicz [see *noskiewiczi* Schwarz] 250
algira Mocsáry [*ruficornis* group] 244
alpha Cockerell [*ruficornis* group] 244
alpina Morawitz [synonym of *obtusifrons* Nylander] 243
alternata (Kirby) [synonym of *goodeniana* (Kirby)] 256
amabilis Radoszkowski [*ruficornis* group] 244
amamiensis Hirashima [*ruficornis* group?] 244
amblystoma Pérez [synonym of *tridentirostris* Dours] 240
americana Kirby [synonym of *articulata* Smith?] 243
amoena Cresson [*ruficornis* group?] 244
amorphae Swenk [*vegana* group] 241
amurensis Radoszkowski [*ruficornis* group] 244
anatolica Pittioni [*ruficornis* group] 244
andalusica Schmiedeknecht [synonym of *basalis* Herrich-Schäffer] 255
angelarum Cockerell [*ruficornis* group] 244
angulata Swenk [*ruficornis* group] 244
annexa Nurse [*ruficornis* group] 244
annularis Olivier [incertae sedis] 258
annulata Smith [*ruficornis* group] 244
anpingensis Strand [*furva* group?] 256
antennata Meade-Waldo [*furva* group] 256
antigana Pérez [synonym of *mutabilis* Morawitz] 253
antonita Cockerell [synonym of *snowii* Cresson] 243
aprilina Swenk [*ruficornis* group] 245
aquilarum Cockerell [*roberjeotiana* group] 242
arasiana Tsuneki [*roberjeotiana* group] 242
arenaria Panzer [incertae sedis] 258
arenicola Swenk [*vegana* group] 241
argentata Herrich-Schäffer [*integra* group] 240
argentea (Schwarz) [*odontophora* group] 241
ariasi Dusmet [*ruficornis* group] 245
arida Nurse [*ruficornis* group] 245
arizonica Cockerell [*ruficornis* group] 245
armata Herrich-Schäffer [*armata* group] 253
armatella Cockerell [*ruficornis* group] 245
arrogans Schmiedeknecht [*ruficornis* group] 245
articulata Smith [*erigeronis* group] 243
ashabadensis Schwarz [*ruficornis* group] 245
ashmeadi Cockerell [*ruficornis* group] 245
asozuana Tsuneki [*ruficornis* group?] 245
astarte Pérez [synonym of *basalis* Herrich-Schäffer] 255
asteris Swenk [*vincta* group] 241
astori Cockerell [*ruficornis* group] 245
aswensis Tsuneki [*ruficornis* group] 245
atrata Smith [synonym of *argentata* Herrich-Schäffer] 240
atrocincta Friese [*furva* group?] 256
atroflava Friese [synonym of *pectoralis* Morawitz] 254
atrofrontata Cockerell [*ruficornis* group] 245
atrohirta Friese [*ruficornis* group?] 245
atroscutellaris Strand [*ruficornis* group] 245
attenuata Cockerell [*furva* group] 256
attrita Cockerell [*furva* group] 256
auctumnalis Ducke [synonym of *trapeziformis* Schmiedeknecht] 252
augustiana Mitchell [*ruficornis* group] 245
aurantiaca Morawitz [synonym of *fulvicornis* Fabricius?] 247
aureopilosa Swenk [subspecies of *rohweri* Cockerell] 244
aurigera Schmiedeknecht [synonym of *fulvicornis* Fabricius] 247

aurolimbata Lozinski [synonym of *fulvicornis* Fabricius] 247
australensis Perkins [*furva* group] 256
australior Cockerell [synonym of *edwardsii edwardsii* Cresson] 254
australis Mitchell [*erigeronis* group] 243
austriaca Schmiedeknecht [synonym of *stigma stigma* Fabricius] 240
autumnalis Mitchell [*ruficornis* group] 245
avalonica Cockerell [*ruficornis* group] 245
azaleae Mitchell [*ruficornis* group] 245
aztecorum Cockerell [*vincta* group] 241
babai Tsuneki [*trispinosa* group?] 256
baccata Smith [*ruficornis* group] 245
baeri Stöckhert [synonym of *castellana* Dusmet] 245
bakeri Cockerell [*furva* group] 256
baldiniana Benzi [incertae sedis] 258
balteata Schmiedeknecht [synonym of *verna* Schmiedeknecht] 253
banahaonis Cockerell [*furva* group] 256
banatica Kiss [synonym of *zonata zonata* Panzer] 253
banksi Cockerell [*ruficornis* group] 245
barbilabris Pérez [*ruficornis* group] 245
barcelonensis Cockerell [*ruficornis* group] 245
basalis Herrich-Schäffer [*basalis* group] 255
basalis Pérez [synonym of *gribodoi* Schmiedeknecht] 248
batava Vollenhoven [synonym of *goodeniana* (Kirby)] 256
beata Nurse [*ruficornis* group] 245
beaumonti Schwarz [*integra* group] 240
belfragei Cresson [*belfragei* group] 254
belikovi Cockerell [synonym of *fulvicornis* Fabricius] 247
bella Cresson [*ruficornis* group] 245
besseyi Swenk [*vincta* group] 241
bethunei Cockerell [*ruficornis* group] 245
beulahensis Cockerell [*ruficornis* group] 245
bicellula Schwarz [*furva* group] 256
bicellularis Ducke [*vegana* group] 241
bicincta Howard [see *bisignata* Say] 245
bicolor Radoszkowski [synonym of *pleurosticta* Herrich-Schäffer] 240
bicrista Swenk [*ruficornis* group] 245
bifasciata Olivier [*bifasciata* group] 255
bifida Thomson [synonym of *ruficornis* Linnaeus] 251
bifurcata Cockerell [*ruficornis* group] 245
biguttata Friese [*furva* group] 256
bilobata Swenk [synonym of *articulata* Smith] 243
bimaculata Eversmann [synonym of *basalis* Herrich-Schäffer] 255
bimaculata Schilling [incertae sedis] 258
binotatus (Robertson) [synonym of *ovata* (Robertson)] 250
bipunctata Fabricius [incertae sedis] 258
bipunctis Pérez [synonym of *conjungens* Herrich-Schäffer] 246
biroi Friese [*furva* group?] 256
bisetosa Swenk [*ruficornis* group] 245
bishoppi Cockerell [*ruficornis* group] 245
bisignata Say [*ruficornis* group] 245
bispinosa Mocsáry [*armata* group] 253
bitincta Alfken [synonym of *obscura* Zetterstedt] 250
blancoburgensis Schmiedeknecht [synonym of *ferruginata* (Linnaeus)] 247
blepharipes Schmiedeknecht [*furva* group] 256
bluethgeni Stöckhert [*furva* group] 256
bofillana Pérez [synonym of *zonata zonata* Panzer] 253
bohartorum Moalif [*vincta* group] 241
bolivari Dusmet [*ruficornis* group?] 245
bonaerensis Holmberg [*vegana* group] 241
borealis Zetterstedt [synonym of *leucophthalma* (Kirby)] 249
bouceki Kocourek [*furva* group] 256
braunsiana Schmiedeknecht [*ruficornis* group] 245
bremensis Alfken [synonym of *fulvicornis* Fabricius] 247
brevicornis Schmiedeknecht [synonym of *argentata* Herrich-Schäffer] 240
brevis Saunders [*trispinosa* group] 256
breviuscula Schwarz [*furva* group] 256
brewsterae Broemeling [*adducta* group] 241
bridgmaniana Smith [synonym of *ferruginata* (Linnaeus)] 247
brunnea Schilling [incertae sedis] 258
brunneofasciata Lozinski [synonym of *fulvicornis* Fabricius] 247
bucephalae Perkins [synonym of *hirtipes* Pérez] 248
buyoo Tsuneki [*roberjeotiana* group?] 242
cabrerai Dusmet [synonym of *barbilabris* Pérez] 245
calabra Morawitz [synonym of *nobilis* Herrich-Schäffer] 255
californiae Cockerell [*ruficornis* group] 245
calimorpha Schmiedeknecht [*ruficornis* group] 245
calloptera Cockerell [*ruficornis* group] 245
calloxantha Cockerell [*ruficornis* group] 245
callura Cockerell [subspecies of *bella* Cresson] 245
capillata Mitchell [*ruficornis* group] 245
capitalis Mitchell [*ruficornis* group] 245
capreae (Kirby) [synonym of *fulvicornis* Fabricius] 247
carcaranensis Cockerell [*vegana* group] 241
carinicauda Cockerell [*ruficornis* group] 245
carnea Friese [synonym of *basalis* Herrich-Schäffer] 255
carnifex Mocsáry [*armata* group] 253
carniolica Schmiedeknecht [synonym of *confinis* Schmiedeknecht] 246
carolinae Cockerell [synonym of *ovata* Robertson] 250
carthaginensis Dusmet [*integra* group] 240
caspia Morawitz [*integra* group] 240
castellana Dusmet [*ruficornis* group] 245
caucasica Lozinski [synonym of *fucata* Panzer] 255
ceanothi Cockerell [*ruficornis* group] 245
ceballosi Dusmet [synonym of *fenestrata fenestrata* Lepeletier] 247
centenarii Dusmet [*ruficornis* group] 245
ceylonica Cameron [*furva* group] 256
cherkesiana Mavromoustakis [*basalis* group] 255
chrysopyga Morawitz [*ruficornis* group] 245
cincta Herrich-Schäffer [synonym of *goodeniana* (Kirby)] 256
cincta Lepeletier [synonym of *mutica* Morawitz] 250
cincta Rossi [incertae sedis] 258
cincticornis Nylander [synonym of *armata* Herrich-Schäffer] 253
cinctiventris Friese [synonym of *integra integra* Brullé] 240
cinnabarina Morawitz [see *stigma stigma* Fabricius] 240
cinnaberina [synonym of *stigma stigma* Fabricius] 240
cirtana Pérez [synonym of *duplex* Smith] 255
citrina Cresson [*ruficornis* group] 246
civilis Cresson [*ruficornis* group] 246
clara Pérez [synonym of *sanguinea* Smith] 254
clarescens Cockerell [*ruficornis* group] 246
clarkii Cockerell [*ruficornis* group] 246
cleopatra Schwarz [*roberjeotiana* group] 243
cockerelli Graenicher [synonym of *aquilarum* Cockerell] 242
coelomeria Pérez [synonym of *sanguinea* Smith] 254
collarae Schwarz [*furva* group] 256
collinsiana Cockerell [*ruficornis* group] 246
coloradella Cockerell [*ruficornis* group] 246
coloradensis Cockerell [*ruficornis* group] 246
colorata Mitchell [*ruficornis* group] 246
comparata Cockerell [*bifasciata* group] 255
composita Mitchell [*ruficornis* group] 246
compta Lepeletier [synonym of *armata* Herrich-Schäffer] 253
concessa Cockerell [*furva* group] 256
concinnula Cockerell [*ruficornis* group] 246
concolor Schmiedeknecht [*ruficornis* group] 246
confinis Schmiedeknecht [*ruficornis* group] 246
conjungens Herrich-Schäffer [*ruficornis* group] 246
connectens Pérez [*furva* group] 256
connexa (Kirby) [synonym of *sexfasciata* Panzer] 255
consobrina Dufour [*ruficornis* group?] 246
conspicua Smith [*furva* group] 256
contractula Cockerell [subspecies of *schwarzi* Cockerell] 252
convolvuli Swenk [synonym of *vierecki* Cockerell] 242

copetica Morawitz [synonym of *calimorpha* Schmiedeknecht] 245
coquilletti Cockerell [*ruficornis* group] 246
corcyraea Schmiedeknecht [*armata* group] 253
corcyrea Pittioni [see *corcyraea* Schmiedeknecht] 253
corcyrea Schwarz [see *corcyraea* Schmiedeknecht] 253
cordilabris Schwarz [*furva* group] 257
cordillera Eardley and Schwarz [*roberjeotiana* group?] 243
cordleyi Cockerell [*ruficornis* group] 246
cornelliana Cockerell [synonym of *perplexa* Cresson] 251
cornigera (Kirby) [synonym of *fulvicornis* Fabricius] 247
coronata Pérez [*furva* group] 257
corvallisensis Cockerell [*erigeronis* group?] 243
costalis Brèthes [*vegana* group] 241
costaricensis Schrottky [*vegana* group] 241
coxalis Morawitz [*ruficornis* group] 246
crassula Cockerell [synonym of *fervida* Smith] 241
crawfordi Cockerell [*ruficornis* group] 246
cressonii Robertson [*ruficornis* group] 246
cretensis Schulz [subspecies of *coxalis* Morawitz] 246
cristata Pérez [*superba* group] 254
crotchii Cresson [*erigeronis* group] 243
crucis Cockerell [*vegana* group] 241
crudelis Cresson [*ruficornis* group] 246
cruenta Schmiedeknecht [*ruficornis* group] 246
cruralis Moure [synonym of *tibialis* Cresson] 242
cubensis Cresson [*vegana* group] 241
cuneata (Robertson) [*ruficornis* group] 246
curvispinosa Schwarz [*furva* group] 257
cushmani Cockerell [synonym of *vierecki* Cockerell] 242
custeriana Cockerell [*ruficornis* group] 246
cymbalariae Cockerell [*ruficornis* group] 246
cyphognatha Pérez [synonym of *tridentirostris* Dours] 240
cypria Mavromoustakis [subspecies of *trispinosa* Schmiedeknecht] 256
cypricola Mavromoustakis [subspecies of *stigma* Fabricius] 240
cypricola Mavromoustakis [*furva* group] 257
dacotana Cockerell [synonym of *articulata* Smith] 243
dacotensis Swenk [synonym of *aquilarum* Cockerell] 242
dahli Friese [*furva* group?] 257
dahlii Curtis [see *sheppardana sheppardana* (Kirby)] 257
daimio Matsumura [synonym of *japonica* Smith] 255
dalii Curtis [synonym of *sheppardana sheppardana* (Kirby)] 257
dallasensis Cockerell [subspecies of *affabilis* Cresson] 254
dallatorreana Schmiedeknecht [synonym of *conjungens* Herrich-Schäffer] 246
danuvia Pittioni [synonym of *goodeniana* (Kirby)] 256
davidsoni Cockerell [*ruficornis* group] 246
debilis Timberlake [*ruficornis* group] 246
decemnotatus (Robertson) [synonym of *cuneata* (Robertson)] 246
decempunctata Cockerell [*ruficornis* group] 246
decepta Mitchell [*ruficornis* group] 246
decorata Markowsky [synonym of *fulvicornis* Fabricius] 247
decorata Smith [synonym of *solitaria* Smith] 252
dentariae (Robertson) [*ruficornis* group] 246
denticulata Robertson [*ruficornis* group] 246
dentipes Rudow [synonym of *femoralis* Morawitz] 253
depressa Cresson [*ruficornis* group] 246
depressicauda Cockerell [synonym of *depressa* Cresson] 246
desertorum Morawitz [synonym of *subvirescens* Morawitz] 255
detecta Nurse [*ruficornis* group] 246
detrita Mitchell [*ruficornis* group] 246
diacantha Schwarz [*furva* group] 257
dialpha Cockerell [subspecies of *alpha* Cockerell] 244
dido Pérez [synonym of *barbilabris* Pérez] 245
diervillae Tsuneki [*ruficornis* group?] 246
difficilis Friese [*superba* group] 254
dilucida Cresson [*ruficornis* group] 246
diluta Gribodo [variety of *fulvicornis* Fabricius] 247
diluta Pérez [synonym of *panzeri* Lepeletier] 250
dira Schmiedeknecht [*ruficornis* group] 246
discedens Pérez [*furva* group] 257
discicollis Morawitz [*ruficornis* group] 246
discrepans Schmiedeknecht [*ruficornis* group] 246
dispar Pérez [synonym of *gribodoi* Schmiedeknecht] 248
dissessa Cockerell [*furva* group] 257
distinguenda Morawitz [*furva* group] 257
dives Erichson [*ruficornis* group?] 246
dolosa Mocsáry [incertae sedis] 258
dreisbachi Mitchell [*ruficornis* group] 246
dreisbachorum Moalif [*vincta* group] 241
dubia Eversmann [*basalis* group] 246
dubia Schmiedeknecht [synonym of *marshamella* (Kirby)] 249
duplex Smith [*bifasciata* group] 255
durangoae Broemeling [*adducta* group] 241
dusmetella Pérez [synonym of *illustris* Schmiedeknecht] 256
dybovskij Radoszkovsky [*ruficornis* group] 246
dzieduszyckii Noskiewicz [synonym of *striata* Fabricius] 252
eastonensis Cockerell [subspecies of *grayi* Cockerell] 248
ecarinata Morawitz [*roberjeotiana* group] 243
ecuadoria Friese [subspecies of *rugicollis* Friese] 242
ednae Cockerell [*ruficornis* group] 246
edwardsii Cresson [*superba* group] 254
electa Cresson [*ruficornis* group] 246
electella Cockerell [*ruficornis* group] 246
elegans Mocsáry [synonym of *gribodoi* Schmiedeknecht] 248
elegantula Cockerell [*roberjeotiana* group] 243
elrodi Cockerell [*ruficornis* group] 246
emarginata Morawitz [*ruficornis* group] 246
emendata Schulz [synonym of *basalis* Herrich-Schäffer] 255
engelmanniae Cockerell [subspecies of *wheeleri* Cockerell] 254
eos Schmiedeknecht [*armata* group] 253
erigeronis Robertson [*erigeronis* group] 244
erigerontis Robertson [see *erigeronis* Robertson] 244
errans Lepeletier [*roberjeotiana* group] 243
erubescens Friese [synonym of *fulvicornis* Fabricius] 247
erythraea Dalla Torre [*ruficornis* group] 246
erythrocephala Morawitz [*furva* group] 257
erythrochroa Cockerell [*erigeronis* group] 244
erythrosoma Mocsáry [synonym of *laticrus* Mocsáry] 257
erythrospila Cockerell [*erigeronis* group] 244
esakii Yasumatsu & Hirashima [*ruficornis* group] 246
esana Tsuneki [*roberjeotiana* group?] 243
etigonis Tsuneki [*roberjeotiana* group?] 243
etizenensis Tsuneki [subspecies of *alboguttata* Herrich-Schäffer] 244
eustalacta Gerstäcker [synonym of *rostrata* Herrich-Schäffer] 251
eversmanni Lozinski [synonym of *fulvicornis* Fabricius] 247
excellens Cockerell [synonym of *hemphilli* Cockerell] 254
excellens Pérez [see *barcelonensis* Cockerell] 245
excisa Pérez [synonym of *bispinosa* Mocsáry] 253
excurrens Cockerell [synonym of *hemphilli* Cockerell] 254
exheredans Cockerell [*furva* group] 257
eximia Eardley & Schwarz [*roberjeotiana* group] 243
fabriciana (Linnaeus) [*ruficornis* group] 246
fabriciella (Kirby) [synonym of *fabriciana* Linnaeus] 247
facilis Schwarz [*integra* group] 240
falconis Rodeck [subspecies of *hesperia* Cockerell] 255
fallax Pérez [*armata* group] 253
fasciata Friese [see *panzeri panzeri* Lepeletier?] 251
fasciculata Morawitz [synonym of *lutea* Eversmann] 249
faventiana Pérez [synonym of *fenestrata fenestrata* Lepeletier] 247
fedtschenkoi Morawitz [*ruficornis* group?] 247
felici Schwarz [*armata* group?, see "*plumosa* assemblage"] 254
femoralis Morawitz [*armata* group] 253
fenestrata Lepeletier [*ruficornis* group] 247
fennica Alfken [synonym of *rufipes* Fabricius] 243
ferghanica Morawitz [*bifasaciata* group?] 255
ferroviaria Dusmet [synonym of *glaucopis* Pérez] 257
ferruginata (Linnaeus) [*ruficornis* group] 247

ferruginea Olivier [incertae sedis] 258
fervens Smith [*ruficornis* group] 247
fervida Smith [*vegana* group] 241
festiva Cresson [*ruficornis* group] 247
festiva Schmiedeknecht [synonym of *italica* Dalla Torre & Friese] 249
flagellaris Cockerell [subspecies of *morrisoni* Cresson] 250
flammigera Cockerell [*ruficornis* group?] 247
flava Panzer [*ruficornis* group] 247
flavescens Friese [synonym of *pampicola* Holmberg?] 242
flavescens Friese [subspecies of *fucata* Panzer] 255
flaviceps Cresson [*vegana* group?] 241
flavicornis Rossi [incertae sedis] 258
flavifrons Dalla Torre [synonym of *sexfasciata* Panzer]
flavilabris Morawitz [*ruficornis* group] 247
flavinervis Brullé [*basalis* group?] 255
flavipes Provancher [synonym of *suavis* Cresson] 242
flavoguttata (Kirby) [*ruficornis* group] 247
flavolimbata Schmiedeknecht [synonym of *fulvicornis* Fabricius] 247
flavomaculata Lucas [synonym of *basalis* Herrich-Schäffer] 255
flavomarginata Swenk [subspecies of *citrina* Cresson] 246
flavopicta (Kirby) [*ruficornis* group] 247
flavopicta Swenk [synonym of *hesperia hesperia* Cockerell] 255
flavopunctata Friese [synonym of *femoralis* Morawitz] 253
flavozonata Nurse [*basalis* group?] 255
floricola Tsuneki [*ruficornis* group] 247
florilega Lovell & Cockerell [*ruficornis* group] 247
fontis Cockerell [*ruficornis* group] 247
formula Viereck [*vegana* group] 241
fowleri Cockerell [synonym of *obscurella* Fowler] 250
fragariae Mitchell [*ruficornis* group] 247
fragilis Cresson [*ruficornis* group] 247
frankei Cockerell [*ruficornis* group] 247
freygesseneri Schmiedeknecht [synonym of *melathoracica* Imhoff] 249
frieseana Cockerell [*erigeronis* group] 244
fucata Panzer [*bifasciata* group] 255
fukuiana Tsuneki [*ruficornis* group] 247
fuliginosa Friese [synonym of *pampicola* Holmberg?] 242
fulvicornis Fabricius [*ruficornis* group; also see *succincta* Panzer] 247
fulvipes Brullé [incertae sedis] 258
furva Panzer [*furva* group] 257
furvoides Stöckhert [*furva* group] 257
fusca Schwarz [*ruficornis* group] 248
fuscicincta Swenk [*ruficornis* group] 248
fuscicornis Nylander [*armata* group] 253
fuscipennis Lepeletier [*superba* group] 254
galloisi Yasumatsu & Hirashima [*roberjeotiana* group] 243
garciana Cockerell [*vegana* group] 241
germanica Fabricius [synonym of *integra* Brullé] 240
germanica Panzer [synonym of *fabriciana* Linnaeus] 247
gerundica Pérez [synonym of *nigrovaria* Pérez] 257
gibbosa Viereck [*ruficornis* group] 248
gigantea Friese [misspelling by Brauns; see *gigas* Friese] 240
gigas Friese [*gigas* group] 240
gillettei Cockerell [*ruficornis* group] 248
ginran Tsuneki [*bifasciata* group?] 256
glabella Thomson [synonym of *panzeri panzeri* Lepeletier] 250
glaberrima Schmiedeknecht [*integra* group] 240
glabriventris Schwarz [*ruficornis* group] 248
glaucopis Pérez [*furva* group] 257
gonzalezi Dusmet [synonym of *melanura* Mocsáry] 249
goodeniana (Kirby) [*bifasciata* group] 256
gracilicornis Morawitz [*ruficornis* group] 248
gracilipes Pérez [synonym of *melanura* Mocsáry] 249
gracilis Cresson [*ruficornis* group] 248
gracillima Lozinski [synonym of *ariasi* Dusmet] 245
graeca Schwarz [synonym of *caspia* Morawitz] 240
graenicheri Cockerell [*ruficornis* group] 248
graja Mocsáry [synonym of *glaberrima* Schmiedeknecht] 240
grandior Friese [*furva* group?] 257
grandis Cresson [*superba* group] 254
gransassoi Schwarz [*ruficornis* group] 248
grayi Cockerell [*ruficornis* group] 248
gribodoi Schmiedeknecht [*ruficornis* group] 248
grossa Friese [synonym of *basalis* Herrich-Schäffer] 255
guichardiana Eardley & Schwarz [*roberjeotiana* group] 243
guichardi Schwarz [*furva* group] 257
gusenleitneri Schwarz [*furva* group] 257
gutierreziae Cockerell [*vegana* group] 241
guttulata Schenck [*ruficornis* group] 248
gyangensis Cockerell [*ruficornis* group] 248
hackoda Tsuneki [*ruficornis* group?] 248
haematodes Schmiedeknecht [synonym of *flavopicta flavopicta* (Kirby)] 247
hakodatensis Tsuneki [*ruficornis* group] 248
hakonensis Cockerell [*ruficornis* group] 248
hakusana Tsuneki [*roberjeotiana* group] 243
hammarstroemi Morawitz [*ruficornis* group] 248
hananoi Yasumatsu & Hirashima [incertae sedis] 258
hanedai Tsuneki [*ruficornis* group?] 248
hangani Tsuneki [synonym of *silvicola* Tsuneki] 252
hararensis Meade-Waldo [*roberjeotiana* group] 243
harimensis Cockerell [*ruficornis* group] 248
heiligbrodti Cresson [*vegana* group] 241
helvetica Schmiedeknecht [synonym of *blepharipes* Schmiedeknecht] 256
hemphilli Cockerell [*superba* group] 254
henningeri Evans [*superba* group] 254
hera Schwarz [*trispinosa* group] 256
herrichschaefferi Strand [synonym of *signata* Jurine?] 252
hesperia Cockerell [*basalis* group?] 255
heterochroa Cockerell [synonym of *vincta* Say] 241
heterosticta Cockerell [*ruficornis* group] 248
hiackogawa Tsuneki [*ruficornis* group?] 248
hillana (Kirby) [synonym of *striata* Fabricius] 252
hipponensis Saunders [synonym of *kohli* Schmiedeknecht] 257
hirsuta Verhoeff [synonym of *flava* Panzer?] 247
hirticeps Pérez [*armata* group?, see "*plumosa* assemblage"] 254
hirtipes Pérez [*ruficornis* group] 248
hirtiventris Schwarz [*furva* group?] 257
hispanica Dusmet [*ruficornis* group] 248
hoeppneri Alfken [synonym of *flavoguttata flavoguttata* (Kirby)] 247
hondurasica Cockerell [*vegana* group] 241
honorata Cockerell [subspecies of *vallesina* Cockerell] 253
hoodiana Cockerell [*ruficornis* group] 248
hrubanti Balthasar (subspecies of *baccata* Smith) 245
hummeli Alfken [*ruficornis* group?] 248
hungarica Dalla Torre & Friese [*ruficornis* group] 248
hurdi Evans, 1972 [*superba* group] 254
hybrida Schmiedeknecht [see *panzeri panzeri* Lepeletier] 251
hydrophylli Swenk [*ruficornis* group] 248
ibanezi Dusmet [*ruficornis* group] 248
iberica Dalla Torre & Friese [synonym of *fucata* Panzer] 256
icazti Tsuneki [*ruficornis* group?] 248
idahoensis Swenk [*ruficornis* group] 248
illinoensis Robertson [*ruficornis* group] 248
illinoënsis Cockerell [see *illinoensis* Robertson] 248
illinoiensis Robertson [see *illinoensis* Robertson] 248
illustris Schmiedeknecht [*bifasciata* group] 256
imbricata Smith [*ruficornis* group] 248
immaculata Morawitz [*armata* group] 253
imperfecta Schwarz [subspecies of *integra* Brullé] 240
imperialis Schmiedeknecht [*superba* group] 254
incerta Cresson [synonym of *articulata* Smith] 243
incisa Schmiedeknecht [*basalis* group] 255
incompleta Schmiedeknecht [see *panzeri panzeri* Lepeletier] 251

inderskiana Lozinski [synonym of *basalis* Herrich-Schäffer] 255
indusata Mitchell [*ruficornis* group] 248
inepta Mitchell [*ruficornis* group] 248
inermis Friese [see *anatolica* Pittioni] 244
inermis Pérez [*ruficornis* group] 248
infantula Cockerell [synonym of *parva* Robertson] 251
infrarubens Cockerell [subspecies of *vicinalis* Cresson] 253
infrequens Smith [*vegana* group] 241
inquilina Smith [synonym of *leucophthalma* Kirby] 249
insignipes Schmiedeknecht [*basalis* group] 255
insularis Smith [*furva* group] 257
integer Robertson [see *integerrima* Dalla Torre] 249
integerrima Dalla Torre [*ruficornis* group] 249
integra Brullé [*integra* group] 240
integra Imhoff [synonym of *goodeniana* (Kirby)] 256
integra Robertson [see *integerrima* Dalla Torre] 249
integricollis Morawitz [incertae sedis] 258
intercepta Smith [synonym of *edwardsii edwardsii* Cresson] 254
intermedia Imhof [synonym of *flava* Panzer] 247
interrupta Fowler [see *interruptella* Fowler] 249
interrupta Panzer [incertae sedis] 258
interruptella Fowler [*ruficornis* group] 249
issikii Yasumatsu [*roberjeotiana* group] 243
italica Dalla Torre & Friese [*ruficornis* group] 249
itamera Cockerell [*ruficornis* group] 249
iwakiyamana Tsuneki [*ruficornis* group?] 253
jacobaeae Panzer [incertae sedis] 258
jamaicensis Cockerell [*vegana* group] 241
jammuensis Schwarz [*ruficornis* group?] 249
japonensis Tsuneki [subspecies of *flavoguttata* (Kirby)] 247
japonica Smith [*basalis* group] 255
jaramensis Dusmet [incertae sedis] 258
jasnitskii Cockerell [synonym of *flavopicta flavopicta* (Kirby)] 247
javanica Friese [*furva* group?] 257
jennei Cockerell [*ruficornis* group] 249
jezoensis Matsumura [subspecies of *fulvicornis* Fabricius] 248
jocularis Cresson [*ruficornis* group] 249
julliani Schmiedeknecht [synonym of *panurgina* Morawitz] 254
jullianii Dalla Torre [see *panurgina* Morawitz] 254
jurassica Stöckhert [synonym of *piccioliana* Magretti] 251
kaguya Hirashima [*ruficornis* group] 249
kaiensis Tsuneki [subspecies of *okamotonis* Matsumura] 243
keroanensis Pérez [*basalis* group] 255
kervilleana Pérez [*ruficornis* group] 249
kincaidiana Cockerell [*ruficornis* group] 249
kingstonensis Mitchell [*ruficornis* group] 249
kinosukei Tsuneki [*ruficornis* group?] 249
kirbyella Stephens [synonym of *armata* Herrich-Schäffer] 253
kirbyi Lepeletier [incertae sedis] 258
klamathensis Fox [*ruficornis* group?] 249
kobrowi Brauns [synonym of *gigas* Friese] 240
kocoureki Schwarz [*trispinosa* group] 256
koebelei Cockerell [*ruficornis* group] 249
kohli Schmiedeknecht [*furva* group] 257
koikensis Tsuneki [*roberjeotiana* group] 243
komarowi Radoszkowski [*ruficornis* group] 249
konowiana Friese [synonym of *flavopicta flavopicta* (Kirby)?] 247
koreana Tsuneki [*ruficornis* group] 249
koreana Cockerell [*ruficornis* group] 249
korleviciana Friese [synonym of *errans* Lepeletier] 243
kornosica Mavromoustakis [*ruficornis* group] 249
kotomaria Tsuneki [*ruficornis* group?] 249
krombeini Schwarz [*ruficornis* group] 249
krueperi Schmiedeknecht [incertae sedis] 258
krugii Cresson [*vegana* group] 241
krüperi Schmiedeknecht [see *krueperi* Schmiedeknecht] 258
kurilensis Yasumatsu [incertae sedis] 258
kuro Tsuneki [*ruficornis* group?] 249
kusdasi Schwarz [*roberjeotiana* group] 243
labiata Olivier [incertae sedis] 258
lachrymosa Cockerell [subspecies of *crawfordi* Cockerell] 246
ladakhiensis Schwarz [*ruficornis* group?] 249
laeta Thomson [synonym of *baccata* Smith] 245
laevilabris Schmiedeknecht [synonym of *sanguinea* Smith] 254
lamarensis Cockerell [*vegana* group] 241
lamellata Schwarz [*armata* group?, see "*plumosa* assemblage"] 254
lanceolata Lepeletier [synonym of *armata* Herrich-Schäffer] 253
laramiensis Swenk [*ruficornis* group] 249
lateralis Panzer [synonym of *ferruginata* (Linnaeus)] 247
lateritia Mocsáry [*basalis* group] 255
lathburiana (Kirby) [*ruficornis* group] 249
laticrus Mocsáry [*furva* group] 257
latifrons Cockerell [*ruficornis* group] 249
latistriga Schmiedeknecht [synonym of *fulvicornis* Fabricius] 248
lebanensis Mavromoustakis [incertae sedis] 258
lehighensis Cockerell [*ruficornis* group] 249
lepeletieri Pérez [subspecies of *bifasciata* Olivier] 255
lepida Cresson [*ruficornis* group] 249
leucophthalma (Kirby) [*ruficornis* group] 249
leucosticta Pérez [subspecies of *insignipes* Schmiedeknecht] 255
leucotricha Strand [*furva* group?] 257
leucozona Rodeck [*ruficornis* group] 249
lewisi Cockerell [*ruficornis* group] 249
libata Cresson [*ruficornis* group] 249
liburnica Friese [synonym of *alboguttata alboguttata* Herrich-Schäffer] 244
limassolica Mavromoustakis [*basalis* group] 255
limata Cresson [*vegana* group] 241
limbata Dalla Torre [see *libata* Cresson] 249
lineola Panzer [synonym of *fulvicornis* Fabricius] 247
lineolata Friese [synonym of *goodeniana* (Kirby)] 256
linsenmaieri Schwarz [*armata* group] 253
linsleyi Evans [*superba* group] 254
lippiae Cockerell [*vegana* group] 242
litigiosa Gribodo [*ruficornis* group] 249
lituripes Pérez [synonym of *carnifex* Mocsáry] 253
longiceps Schmiedeknecht [synonym of *rostrata* Herrich-Schäffer] 251
longicornis Friese [*furva* group?] 257
louisianae Cockerell [*ruficornis* group] 249
lucidula Schwarz [*superba* group] 254
lucifera Schmiedeknecht [synonym of *mutabilis* Morawitz] 253
lucilla Nurse [*furva* group] 257
lusca Smith [*furva* group] 257
lutea Eversmann [*ruficornis* group?] 249
luteola Olivier [*ruficornis* group?] 249
luteoloides Robertson [*ruficornis* group] 249
luteopicta Cockerell [*ruficornis* group] 249
lynesi Cockerell [synonym of *mauritanica mauritanica* Lepeletier] 256
macrocardia Pérez [synonym of *sabulosa* Radoszkowski] 252
maculata Cresson [*ruficornis* group] 249
maculicornis Pérez [*ruficornis* group] 249
maculifrons Smith [*ruficornis* group] 249
maculipennis (Cameron) [*ruficornis* group] 249
maculipennis Friese [*ruficornis* group?] 249
maculiscapa Pérez [synonym of *thersites* Schmiedeknecht] 240
maculiventer Swenk [*ruficornis* group] 249
magnifica Cockerell [synonym of *grandis* Cresson] 254
magrettiana Schmiedeknecht [synonym of *nobilis* Herrich-Schäffer] 255
major Morawitz [synonym of *pleurosticta* Herrich-Schäffer] 240
makilingensis Cockerell [*furva* group] 257
malayana Cameron [*furva* group] 257
malonella Cockerell [*ruficornis* group?] 249
malonina Cockerell [*erigeronis* group?] 244
malvastri Swenk [subspecies of *superba* Cresson] 255
mamillaris Pérez [synonym of *chrysopyga pyrosoma* Dours] 245

mamiyai Tsuneki [*ruficornis* group?] 249
manni Morawitz [subspecies of *mauritanica* Lepeletier] 256
margelanica Schwarz [*ruficornis* group] 249
margnella Cockerell [*roberjeotiana* group?] 243
maroccana Pérez [subspecies of *fulvicornis* Fabricius] 248
marshamella (Kirby) [*ruficornis* group] 249
martinella Cockerell [*erigeronis* group] 244
mauritanica Lepeletier [*bifasciata* group] 256
mckenziei Timberlake & Cockerell [*roberjeotiana* group] 243
media Mitchell [*ruficornis* group] 249
mediana Swenk [*ruficornis* group] 249
megacephala Schenck [synonym of *fuscicornis* Nylander] 253
megapolitanica Schmiedeknecht [synonym of *ferruginata* (Linnaeus)] 247
melanocera Gribodo [synonym of *fulvicornis* Fabricius] 248
melanoptera Cockerell [*vegana* group] 242
melanopyga Schmiedeknecht [*bifasciata* group] 256
melanoscapa Gribodo [synonym of *duplex* Smith] 255
melanosoma Cockerell [*roberjeotiana* group] 243
melanostoma Herrich-Schäffer [incertae sedis] 258
melanothorax Schmiedeknecht [synonym of *fulvicornis* Fabricius] 248
melanura Mocsáry [*ruficornis* group] 249
melanura Tsuneki [see *hakusana* Tsuneki] 243
melathoracica Imhoff [*ruficornis* group] 249
melitensis Costa [incertae sedis] 258
melliventris Cresson [*erigeronis* group] 244
mendica Mitchell [*ruficornis* group] 249
mephisto Schmiedeknecht [synonym of *mauritanica mauritanica* Lepeletier] 256
mera Cockerell [synonym of *cressonii cressonii* Robertson] 246
merceti Alfken [*armata* group] 253
meridionalis Schmiedeknecht [synonym of *fulvicornis* Fabricius] 248
mesosticta Cockerell [subspecies of *fragilis* Cresson] 247
mexicana Cresson [*vegana* group] 242
meyeri Dusmet [synonym of *brevis* Saunders] 256
micronycha Pérez [*ruficornis* group] 250
microsticta Cockerell [synonym of *sheppardana minuscula* Noskiewicz] 257
miensis Tsuneki [synonym of *koebelei* Cockerell] 249
mimula Cockerell [synonym of *electa* Cresson] 246
mimus (Cockerell) [*vegana* group?] 242
mindanaonis Cockerell [*furva* group] 257
miniata Smith [*ruficornis* group] 250
minima Mitchell [*ruficornis* group?] 250
minor Gmelin [*ruficornis* group?] 250
minuscula Noskiewicz [subspecies of *sheppardana* (Kirby)] 257
minuta Fabricius [synonym of *flavoguttata flavoguttata* (Kirby)] 247
minuta Swenk [see *swenki* Schwarz] 252
minutula Friese [synonym of *rufipes* Fabricius] 243
mirabilis Schmiedeknecht [synonym of *signata* Jurine] 252
miranda Schmiedeknecht [synonym of *flavopicta flavopicta* (Kirby)] 247
mishimana Tsuneki [*ruficornis* group?] 250
mistura Smith [synonym of *obtusifrons* Nylander] 243
mitchelli Cockerell [*vegana* group] 242
mixta Dalla Torre [synonym of *succincta* Panzer] 256
mixtella Noskiewicz [synonym of *posthuma* Blüthgen] 257
mocsaryi Schmiedeknecht [*basalis* group] 255
modesta Cresson [synonym of *vegana* Cockerell] 242
modesta Herrich-Schäffer [see *panzeri panzeri* Lepeletier] 251
modesta Schmiedeknecht [synonym of *marshamella* (Kirby)] 249
modocorum Cockerell [synonym of *ultima* Cockerell] 252
moeschleri Alfken [*ruficornis* group] 250
momoglonis Tsuneki [see *hakusana* Tsuneki] 243
monozona Friese [*furva* group?] 257
montana (Mocsáry) [synonym of *roberjeotiana roberjeotiana* Panzer] 243
montana (Scopoli) [synonym of *ferruginata* (Linnaeus)] 247
montarcosi Dusmet [subspecies of *barcelonensis* Cockerell] 245
montezumia Smith [synonym of *limata* Cresson] 242
montverna Tsuneki [*ruficornis* group?] 250
moravitzii Radoszkowski [*superba* group] 254
morawitzi Pérez (synonym of *pleurosticta* Herrich-Schäffer) 240
moricei Friese [*odontophora* group] 241
morio Swederus [incertae sedis] 258
morrisoni Cresson [*ruficornis* group] 250
muinensis Tsuneki [*ruficornis* group?] 250
multicolor Ducke [*vegana* group?] 242
multispinosa Saunders [synonym of *polyacantha* Pérez] 254
munakatai Tsuneki [*roberjeotiana* group?] 243
munda Cresson [*ruficornis* group] 250
murotai Tsuneki [*ruficornis* group?] 250
mutabilis Morawitz [*armata* group] 253
mutans Cockerell [*roberjeotiana* group] 243
mutica Morawitz [*ruficornis* group] 250
mutsuensis Tsuneki [*ruficornis* group?] 250
nana Schenck [synonym of *flavoguttata flavoguttata* (Kirby)] 247
nanaensis Tsuneki [*ruficornis* group?] 250
nasuta Scopoli [incertae sedis] 258
nausicaa Schmiedeknecht [*armata* group] 254
navasi Dusmet [synonym of *bifasciata lepeletieri* Pérez] 255
nebrascensis Swenk [synonym of *superba malvastri* Swenk] 255
neglecta Herrich-Schäffer [synonym of *roberjeotiana roberjeotiana* Panzer] 243
neomexicana Cockerell [*vegana* group] 242
nepalensis Schwarz [*furva* group?] 257
nesiotica Mavromoustakis [*basalis* group] 255
nigella Nylander [incertae sedis] 258
nigra Schwarz [subspecies of *integra* Brullé] 240
nigrescens Friese [synonym of *biroi* Friese?] 256
nigrescens Friese [*vegana* group] 242
nigricans Schmiedeknecht [subspecies of *furva* Panzer?] 257
nigricollis Morawitz [incertae sedis] 258
nigricornis Olivier [synonym of *fabriciana* (Linnaeus)] 247
nigrina Lozinski [synonym of *fulvicornis* Fabricius] 248
nigrior Cockerell [subspecies of *crotchii* Cresson] 244
nigrita Pérez [synonym of *chrysopyga pyrosoma* Dours] 245
nigrita Schenck [synonym of *fabriciana* (Linnaeus)] 247
nigriventris Alfken [synonym of *rufipes* Fabricius] 243
nigroantennata Schmiedeknecht [synonym of *similis* Morawitz] 254
nigrociliata Swenk [*ruficornis* group] 250
nigrocincta Smith [*ruficornis* group] 250
nigrofasciata Swenk [*ruficornis* group] 250
nigroflavida Gribodo [synonym of *duplex* Smith] 255
nigropalliata Hedicke [incertae sedis] 258
nigrorufa Retzius [incertae sedis] 258
nigrovaria Pérez [*furva* group] 257
nipponica Yasumatsu & Hirashima [*trispinosa* group] 256
nitescens Cockerell [synonym of *vegana* Cockerell] 242
nitida Schwarz [*armata* group] 254
nitidiceps Cockerell [*vegana* group] 242
nobilis Herrich-Schäffer [*basalis* group] 255
noskiewiczi Schwarz [*ruficornis* group] 250
novioregensis Pérez [synonym of *piccioliana* Magretti] 251
numida Lepeletier [synonym of *mauritanica* Lepeletier] 256
nunobensis Tsuneki [*ruficornis* group?] 253
nuptialis Noskiewicz [synonym of *flavilabris* Morawitz] 247
nuptura Dusmet [synonym of *hispanica* Dusmet] 248
nurukawa Tsuneki [*ruficornis* group?] 250
obburdinensis Morawitz [*ruficornis* group] 250
obliqua Fowler [synonym of *obliquella* Fowler] 250
obliqua Olivier [incertae sedis] 258
obliquella Fowler [*ruficornis* group] 250
obliterata Cresson [*ruficornis* group] 250
obscura Fowler [synonym of *obscurella* Fowler] 250
obscura Zetterstedt [*ruficornis* group] 250

obscurata Schmiedeknecht [subspecies of *stigma* Fabricius] 240
obscurella Fowler [*ruficornis* group] 250
obscuriventris Schwarz [*ruficornis* group?] 250
obstusata Swenk [see *obtusata* Swenk] 250
obtusata Swenk [*ruficornis* group] 250
obtusifrons Nylander [*roberjeotiana* group] 243
ochlerata Mitchell [*ruficornis* group] 250
ochrohirta Swenk [*ruficornis* group] 250
ochrostoma (Kirby) [synonym of *striata* Fabricius] 252
ochrostoma Zetterstedt [synonym of *alboguttata alboguttata* Herrich-Schäffer] 244
octomaculatus (Robertson) [synonym of *ovata* (Robertson)] 250
octonotatus (Robertson) [synonym of *cuneata* (Robertson)] 246
oculata Friese [*superba* group] 254
odontocera Cockerell [*ruficornis* group] 250
odontophora Kohl [*odontophora* group] 241
ohnonis Tsuneki [*ruficornis* group?] 250
oirasensis Tsuneki [subspecies of *osimana* Tsuneki] 250
okamotonis Matsumura [*roberjeotiana* group] 243
okubira Tsuneki [subspecies of *sheppardana* (Kirby)] 257
olhae Cockerell [synonym of *pulchra* Arnold] 251
olympica Schmiedeknecht [synonym of *mutica* Morawitz] 250
omahaensis Swenk [synonym of *snowii* Cresson] 243
opaca Alfken [*ruficornis* group] 250
opacella Timberlake [*ruficornis* group] 250
opposita Cresson [*ruficornis* group] 250
oralis Schwarz [*furva* group] 257
orba Mitchell [*ruficornis* group] 250
orbitalis Pérez [*furva* group] 257
orcusella Cockerell [*ruficornis* group?] 250
oregonica Cockerell [*ruficornis* group] 250
orenburgensis Lozinski [subspecies of *ruficornis* (Linnaeus)] 251
orientalis Yasumatsu & Hirashima [synonym of *harimensis* Cockerell] 248
orientis Tsuneki [subspecies of *panzeri* Lepeletier] 251
ornata Eversmann [incertae sedis] 258
ornithica Cockerell [*ruficornis* group] 250
orophila Cockerell [*ruficornis* group] 250
ortegai Dusmet [*integra* group] 240
osborni Cockerell [*ruficornis* group] 250
osimana Tsuneki [*ruficornis* group?] 250
ovaliceps Schwarz [*furva* group] 257
ovata (Robertson) [*ruficornis* group] 250
pacata Cresson [synonym of *accepta* Cresson] 244
pacifica Tsuneki [*ruficornis* group] 250
packardiella Cockerell [*ruficornis* group] 250
palaciosi Dusmet [synonym of *melanura* Mocsáry] 249
palavanica Cockerell [*furva* group] 257
pallescens Herrich-Schäffer [see *alboguttata alboguttata* Herrich-Schäffer] 258
pallidella Cockerell [*ruficornis* group] 250
pallidelutea Swenk [*vegana* group] 242
pallidenotata Schmiedeknecht [*ruficornis* group] 250
pallidipicta Swenk [*ruficornis* group] 250
pallispinosa Schwarz [*integra* group] 240
palmeni Morawitz [*roberjeotiana* group] 243
pampicola Holmberg [*vegana* group] 242
panamensis Michener [*vegana* group] 242
panurgina Morawitz [*armata* group] 254
panurginoides Saunders [*armata* group] 254
panzeri Lepeletier [*ruficornis* group] 250
panzeriana Walckenaer [synonym of *roberjeotiana roberjeotiana* Panzer] 243
papuana Cockerell [*furva* group] 257
parallela Swenk [*ruficornis* group] 251
paralpha Cockerell [subspecies of *alpha* Cockerell] 244
parata Cresson [*ruficornis* group] 251
parkeri Evans [*superba* group] 254
parva Friese [synonym of *flavopicta flavopicta* (Kirby)?] 247
parva Robertson [*ruficornis* group] 251
parvula De Stefani [see *siciliensis* Dalla-Torre & Friese] 256
parvula (Holmberg) [synonym of *bicellularis* Ducke] 241
parvula Lucas [incertae sedis] 258
pascoensis Cockerell [*erigeronis* group] 244
pastoralis Eversmann [*ruficornis* group] 251
pastoralis Schmiedeknecht [synonym of *ariasi* Dusmet] 245
pecosensis Cockerell [*superba* group] 254
pectoralis Morawitz [*superba* group] 254
pekingensis Tsuneki [*bifasciata* group?] 256
penangensis Cockerell [*furva* group] 257
peninsularis Cockerell [synonym of *pallidelutea* Swenk] 242
perbella (Viereck) [*ruficornis* group] 251
perezi Dusmet [incertae sedis] 258
perivincta Cockerell [*ruficornis* group] 251
perplexa Cresson [*ruficornis* group] 251
perplexans Cockerell [*ruficornis* group] 251
persica Dusmet [incertae sedis] 258
pervasor Cockerell [*furva* group] 257
pesenkoi Schwarz [*basalis* group] 255
pharaonis Friese [synonym of *chrysopyga pyrosoma* Dours] 245
phoenicia Schmiedeknecht [see *panzeri panzeri* Lepeletier] 251
physura Cockerell [*ruficornis* group] 251
piccioliana Magretti [*ruficornis* group] 251
picta (Kirby) [synonym of *rufipes* Fabricius] 243
picticauda Cockerell [*furva* group] 257
pictiscutum Alfken [*superba* group] 254
pilipes (Cresson) [*vegana* group] 242
piliventris Morawitz [*ruficornis* group] 251
pintosi Dusmet [synonym of *fulvicornis maroccana* Pérez] 248
placida Cresson [*roberjeotiana* group] 243
placitensis Cockerell [*ruficornis* group] 251
planifrons Lozinski [incertae sedis] 258
planiscuta Saunders [synonym of *bifasciata bifasciata* Olivier] 255
platythorax Schwarz [*ruficornis* group] 251
platyventris Morawitz [*ruficornis* group] 251
platyzona Pérez, 1884 [synonym of *algira* Mocsáry] 244
plenus (Robertson) [synonym of *ovata* (Robertson)] 250
pleurosticta Herrich-Schäffer [*integra* group] 240
plumosa Gribodo [*armata* group?, see "*plumosa* assemblage"] 254
podagrica Gribodo [*superba* group] 254
poecilonota Pérez [synonym of *mauritanica mauritanica* Lepeletier] 256
polemediana Mavromoustakis [*trispinosa* group] 256
polyacantha Pérez [*armata* group] 254
polybioides Ducke [*vegana* group?] 242
polyodonta Cockerell [*furva* group] 257
portalensis Broemeling [*adducta* group] 241
posthuma Blüthgen [*furva* group?] 257
poultoni Saunders [synonym of *mauritanica mauritanica* Lepeletier] 256
praestans Saunders [synonym of *dira* Schmiedeknecht] 246
pratensis Cockerell [subspecies of *aztecorum* Cockerell] 241
pretiosa Friese [synonym of *fucata fucata* Panzer] 256
priesneri Schwarz [*furva* group] 257
priscilla Nurse [*furva* group] 257
propinqua Schmiedeknecht [*ruficornis* group] 251
propinqua Swenk [see *krombeini* Schwarz] 249
proteus Lepeletier [synonym of *flava* Panzer] 247
proxima Cresson [*ruficornis* group] 251
pruinosa Pérez [*armata* group] 254
pseudops Cockerell [*ruficornis* group] 251
psilocera Kohl [*furva* group] 257
pulawskii Tsuneki [*furva* group] 257
pulchella Smith [synonym of *obliterata* Cresson?] 250
pulcherrima Stöckhert [subspecies of *zonata* Panzer] 253
pulchra Arnold [*ruficornis* group] 251
pulsatillae Cockerell [*ruficornis* group] 251
punctata Lepeletier [incertae sedis] 258
punctata Smith [synonym of *fulvicornis robusta* Fabricius] 248

punctigera Dalla Torre [synonym of *fulvicornis robusta* Fabricius] 248
punctiscuta Thomson [synonym of *striata* Fabricius] 252
punctulifera Friese [synonym of *rufipes* Fabricius] 243
pusilla Pérez et pl. auctt. [see *bifasciata bifasciata* Olivier] 255
pusilla Lepeletier [synonym of *glaucopis* Pérez] 257
pusilla Rossi [incertae sedis] 258
putnami Cresson [*vegana* group] 242
pygidialis Schwarz [*ruficornis* group] 251
pygmaea Cresson [*ruficornis* group] 251
pygmaea Schenck [synonym of *flavoguttata flavoguttata* (Kirby)] 247
pyrifera Cockerell [*ruficornis* group] 251
pyrosoma Dours [subspecies of *chrysopyga* Morawitz] 245
pyrrha Cockerell [*ruficornis* group] 251
quadridens Pérez [synonym of *concolor* Schmiedeknecht] 246
quadrifasciata Schwarz [*ruficornis* group] 251
quadrimaculatus (Robertson) [synonym of *ovata* (Robertson)] 250
quadrinotata (Kirby) [synonym of *fabriciana* (Linnaeus)] 247
quadrisignatus (Robertson) [synonym of *cuneata* (Robertson)] 246
quadrispinosa Mocsáry [incertae sedis] 258
quadrivittata Lozinski [synonym of *fulvicornis* Fabricius] 248
quinquefasciata Schwarz [*superba* group] 254
quinquespinosa Thomson [synonym of *alboguttata alboguttata* Herrich-Schäffer] 244
radiata Nurse [*ruficornis* group] 251
radoszkowskii Lozinski [*ruficornis* group] 251
rakosiensis Friese [synonym of *fulvicornis fulvicornis* Fabricius?] 248
ranunculi Scopoli [incertae sedis] 258
regalis Morawitz [synonym of *basalis* Herrich-Schäffer] 255
regina Friese [*basalis* group?] 255
rengnio Tsuneki [*ruficornis* group] 251
rhenana Morawitz [*ruficornis* group] 251
rhinula Strand [*furva* group?] 257
rhodalis Cockerell [*ruficornis* group] 251
rhodomelas Cockerell [*ruficornis* group] 251
rhodosoma Cockerell [*ruficornis* group] 251
rhodosomella Cockerell [subspecies of *rhodosoma* Cockerell] 251
rhodotricha Cockerell [*superba* group] 254
rhodoxantha Cockerell [*ruficornis* group] 251
ridingsii Cresson [*vegana* group] 242
risiriensis Tsuneki [*ruficornis* group?] 251
rivalis Cresson [*ruficornis* group] 251
rivertonensis Cockerell [synonym of *heiligbrodti* Cresson] 241
roberjeotiana Panzer [*roberjeotiana* group] 243
robertsonella Cockerell [*ruficornis* group] 251
robusta Morawitz [synonym of *fulvicornis* Fabricius] 248
rodecki Mitchell [*rodecki* group] 244
rohweri Cockerell [*erigeronis* group] 244
romana Friese [*ruficornis* group?] 251
rossica Schmiedeknecht [synonym of *fulvicornis* Fabricius] 248
rostrata Herrich-Schäffer [*ruficornis* group] 251
rostrata Lepeletier [synonym of *armata* Herrich-Schäffer] 253
rubescens Lozinski [synonym of *cruenta sexspinosa* Friese] 246
rubi Swenk [*ruficornis* group] 251
rubicunda Olivier [*erigeronis* group] 244
rubiginosa Pérez [*integra* group] 240
rubra Eversmann [see *fulvicornis robusta* Morawitz] 248
rubra (Geoffrey) [see *panzeri* Lepeletier] 251
rubra Provancher [see *erythraea* Dalla Torre] 246
rubra Smith [synonym of *basalis* Herrich-Schäffer] 255
rubrella Cockerell [*ruficornis* group] 251
rubrica Provancher [*ruficornis* group?] 251
rubricata Stöckhert [subspecies of *zonata* Panzer] 253
rubricollis Schwarz [*integra* group] 240
rubricosa Eversmann [*ruficornis* group] 251
rubricoxa Schwarz [*armata* group] 254
rubriventris Schwarz [*ruficornis* group] 251
rubrolineata Pittioni [see *chrysopyga pyrosoma* Dours] 245
rufa Rossi [incertae sedis] 258
rufescens Scopoli [incertae sedis] 258
ruficeps Lepeletier [incertae sedis] 258
ruficollis Morawitz [*ruficornis* group] 251
ruficornis (Linnaeus) [*ruficornis* group] 251
ruficornis Scopoli [incertae sedis] 258
ruficrus Stöckhert [synonym of *fabriciana* (Linnaeus)] 247
rufilabris Thomson [synonym of *guttulata* Schenck] 248
rufinasutina Strand [incertae sedis] 258
rufipes Fabricius [*roberjeotiana* group] 243
rufipes Schenck [synonym of *rhenana* Morawitz] 251
rufiventris (Kirby) [synonym of *lathburiana* (Kirby)] 249
rufiventris Spinola [incertae sedis] 258
rufoabdominalis Schwarz [*armata* group] 254
rufocincta Kirby [synonym of *flavoguttata flavoguttata* (Kirby)] 247
rufohirta Morawitz [incertae sedis] 258
rufomaculata Lozinski [synonym of *fulvicornis* Fabricius] 248
rufopicta (Kirby) [synonym of *rufipes* Fabricius] 243
rufopleurae Schwarz [subspecies of *fenestrata* Lepeletier] 247
rufosoma Strand [incertae sedis] 258
rufula Cockerell [subspecies of *citrina* Cresson] 246
rufula Friese [variety of *succincta* Panzer?] 256
rugicollis Friese [*vegana* group?] 242
rugithorax Pérez [synonym of *distinguenda* Morawitz] 257
ruidosensis Cockerell [*ruficornis* group] 251
sabaensis Tsuneki [*ruficornis* group] 251
sabulosa Radoszkowski [*ruficornis* group] 251
sagana Mocsáry [synonym of *dira* Schmiedeknecht] 246
sagemehli Schmiedeknecht [synonym of *fulvicornis* Fabricius] 248
sagemehlii Dalla Torre [see *sagemehli* Schmiedeknecht] 248
sakura Tsuneki [*ruficornis* group?] 252
salicicola Swenk [*ruficornis* group] 252
salicis Robertson [*ruficornis* group] 252
saltillo Broemeling [*vincta* group] 241
samarcandica Friese [*basalis* group?] 255
sanctaecrucis Cockerell [*ruficornis* group] 252
sandacana Cockerell [*furva* group] 257
sanguinea Smith [*armata* group] 254
sanguinicollis Friese [*ruficornis* group?] 252
sanguinolenta Friese [synonym of *pampicola* Holmberg?] 242
sardiniensis Friese [synonym of *duplex* Smith] 255
sarmatica Stöckhert [subspecies of *zonata* Panzer] 253
sarta Morawitz [*ruficornis* group?] 252
sayi Robertson [*ruficornis* group] 252
schaefferella (Kirby) [synonym of *sexfasciata* Panzer] 255
schaefferi Dufour [incertae sedis] 258
scheviakovi Cockerell [synonym of *goodeniana* (Kirby)] 256
schmiedeknechti Schmiedeknecht [synonym of *fulvicornis* Fabricius] 248
schwarzi Cockerell [*ruficornis* group] 252
scita Cresson [*erigeronis* group] 244
scita Schmiedeknecht [see *hungarica* Dalla Torre & Friese] 248
scitiformis Cockerell [*erigeronis* group] 244
scutellaris Morawitz [synonym of *ferghanica* Morawitz] 255
scutellaris Olivier [incertae sedis] 258
scutellata Friese [*bifasciata* group?] 256
scutellata Saunders [synonym of *chrysopyga pyrosoma* Dours] 245
secessa Cockerell [*furva* group?] 257
sedae Cockerell [synonym of *sedi* Cockerell] 252
sedi Cockerell [*ruficornis* group] 252
semenowi Morawitz [synonym of *komarowi* Radoszkowski] 249
semirufula Cockerell [subspecies of *perivincta* Cockerell] 251
semirugosa Cockerell [*ruficornis* group] 252
semiscita Cockerell [*erigeronis* group] 244
semisuavis Cockerell [*vegana* group] 242

sempiterna Morawitz [*roberjeotiana* group] 243
seneciophila Mitchell [*erigeronis* group] 244
septentrionalis Swenk [subspecies of *ultimella* Cockerell] 252
sericea Dufour [incertae sedis] 258
sericultorum Schulz [see *chrysopyga chrysopyga* Morawitz] 245
serotina Schmiedeknecht [synonym of *flavoguttata flavoguttata* (Kirby)] 247
serricornis Pérez [*armata* group (in part)] 254
sexcincta (Kirby) [synonym of *fulvicornis* Fabricius] 248
sexfasciata Panzer [*superba* group] 254
sexmaculatus (Robertson) [synonym of *ovata* (Robertson)] 250
sexnotatus (Robertson) [synonym of *cuneata* (Robertson)] 246
sexspinosa Friese [subspecies of *cruenta* Schmiedeknecht] 246
sheppardana (Kirby) [*furva* group] 257
shimoyamai Tsuneki [synonym of *osmana oirasensis* Tsuneki] 250
shirakii Yasumatsu & Hirashima [*ruficornis* group] 252
shoyozana Tsuneki [*ruficornis* group?] 252
sibirica Friese [synonym of *errans* Lepeletier] 243
sibirica Mocsáry [synonym of *fulvicornis* Fabricius] 248
siccorum Cockerell [*ruficornis* group] 252
siciliensis Dalla-Torre & Friese [*bifasciata* group?] 256
sicula Schwarz [*armata* group] 254
signata Jurine [*ruficornis* group] 252
silvicola Tsuneki [*ruficornis* group] 252
similis Morawitz [*armata* group] 254
simillima Pérez [synonym of *striata* Fabricius] 252
simplex Robertson [synonym of *denticulata* Robertson] 246
simplicicoxa Swenk [*vegana* group] 242
siouxensis Swenk [*ruficornis* group] 252
skinneri Cockerell [*ruficornis* group] 252
slovakica [synonym of *stigma stigma* Fabricius] 240
smyrnaensis Friese [*furva* group?] 257
snowii Cresson [*roberjeotiana* group] 243
sobrina Mitchell [*ruficornis* group] 252
solidaginis Panzer [synonym of *rufipes* Fabricius] 243
solitaria Smith [*ruficornis* group] 252
sophiarum Cockerell [*erigeronis* group] 244
speciosissima Schmiedeknecht [synonym of *chrysopyga chrysopyga* Morawitz] 245
sphaerogaster Cockerell [*ruficornis* group] 252
spinicoxa Schwarz [*roberjeotiana* group] 243
spokanensis Cockerell [subspecies of *civilis* Cresson] 246
squalida Scopoli [incertae sedis] 258
sternalis Pérez [*armata* group?] 254
stevensi Swenk [subspecies of *vicina* Cresson] 253
stigma Fabricius [*integra* group] 240
stoeckherti Pittioni [*ruficornis* group] 252
striata Fabricius [*ruficornis* group] 252
strigicollis Morawitz [subspecies of *fulvicornis* Fabricius] 248
suavis Cresson [*vegana* group] 242
subaccepta Cockerell [*ruficornis* group] 252
subangusta Cockerell [*ruficornis* group] 252
subcornuta (Kirby) [synonym of *fulvicornis* Fabricius] 248
subfasciata Schilling [incertae sedis] 258
subgracilis Cockerell [*ruficornis* group] 252
sublippiae Cockerell [subspecies of *lippiae* Cockerell] 242
subnigrocincta Swenk [*ruficornis* group] 252
subpacata Swenk [*ruficornis* group] 252
subpetiolata Smith [*furva* group] 257
subrubi Swenk [*ruficornis* group] 252
subrutila Lovell and Cockerell [*ruficornis* group] 252
subscopifera Ducke [*vegana* group?] 242
subsimilis Cockerell [*ruficornis* group] 252
subvicinalis Cockerell [*ruficornis* group] 252
subvirescens Morawitz [*basalis* group] 255
succincta Panzer [*bifasciata* group] 256
succincta Scopoli [incertae sedis] 258
suda Cresson [*ruficornis* group] 252
sudai Tsuneki [*ruficornis* group?] 252
suerinensis Friese [synonym of *alboguttata alboguttata* Herrich-Schäffer] 244
suffossa Cockerell [*vincta* group] 241
sulphurata Smith [*ruficornis* group] 252
sulphuripes Morawitz [incertae sedis] 258
sunayamana Tsuneki [*ruficornis* group?] 252
superba Cresson [*superba* group] 255
superba Pérez [synonym of *chrysopyga chrysopyga* Morawitz] 245
sutepensis Cockerell [*furva* group] 257
swenki Schwarz [*ruficornis* group] 252
sybarita Schmiedeknecht [*basalis* group] 255
symphyti Stöckhert [*ruficornis* group] 252
syriaca Dusmet [incertae sedis] 258
syriaca Friese [synonym of *chrysopyga chrysopyga* Morawitz] 245
taeniata Gribodo [synonym of *fucata fucata* Panzer] 256
taicho Tsuneki [*furva* group] 257
talyschiensis Morawitz [incertae sedis] 258
taraxacella Cockerell [*ruficornis* group] 252
temmasana Tsuneki [*roberjeotiana* group?] 243
tenella Mocsáry [*ruficornis* group] 252
tenuicornis Cockerell [*vegana* group] 242
tepoztlan Moalif [*vincta* group] 241
terminalis Imhoff [incertae sedis] 258
testaceobalteata Cameron [*furva* group] 257
texana Cresson [*vegana* group] 242
thersites Schmiedeknecht [*integra* group] 240
thoracica Morawitz [incertae sedis] 258
tibialis Cresson [*vegana* group] 242
tiendang Tsuneki [*roberjeotiana* group?] 243
tiftonensis Cockerell [synonym of *heiligbrodti* Cresson] 241
tigridis Morice [incertae sedis] 258
timberlakei Broemeling [*roberjeotiana* group] 243
tintinnabulum Cockerell [*ruficornis* group] 252
tomentifera Ducke [*vegana* group?] 242
tormentillae Alfken [synonym of *roberjeotiana roberjeotiana* Panzer] 243
torrida Smith [synonym of *rubicunda* Olivier] 244
towada Tsuneki [*ruficornis* group] 252
townesi Mitchell [*ruficornis* group?] 252
tranquebarorum (Swederus) [incertae sedis] 258
transitoria Schmiedeknecht [*armata* group] 254
transsylvanica Endre [synonym of *errans* Lepeletier] 243
trapeziformis Schmiedeknecht [*ruficornis* group] 252
trapidoi Michener [*vegana* group] 242
trevoriana Cockerell [subspecies of *cressonii* Robertson] 246
tricolor Brullé [synonym of *basalis* Herrich-Schäffer] 255
tricurta Swenk [*ruficornis* group] 252
tridentata Tsuneki [*ruficornis* group?] 253
tridentilabris Schwarz [synonym of *carnifex* Mocsáry] 253
tridentirostris Dours [*integra* group] 240
tripunctata Morawitz [synonym of *basalis* Herrich-Schäffer] 255
trispinosa Schmiedeknecht [*trispinosa* group] 256
truttarum Cockerell [*ruficornis* group] 252
tuberculata Lepeletier [incertae sedis] 258
tunetana Dusmet [incertae sedis] 258
turneri Meade-Waldo [*furva* group] 257
tyrellensis Mitchell [*ruficornis* group] 252
uhleri Cockerell [*vegana* group] 242
ulsterensis Mitchell [*ruficornis* group] 252
ultima Cockerell [*ruficornis* group] 252
ultimella Cockerell [*ruficornis* group] 252
umbripennis Alfken [synonym of *chrysopyga pyrosoma* Dours] 245
umbrosa Schmiedeknecht [subspecies of *braunsiana* Schmiedeknecht] 245
undulaticornis Cockerell [*ruficornis* group] 252
unicolor (Robertson) [synonym of *ovata* (Robertson)] 250
unifasciata Schilling [incertae sedis] 258
unispinosa Schwarz [*armata* group] 254

utahensis Moalif [*vincta* group] 241
utensis Swenk [*ruficornis* group] 252
uzensis Tsuneki [*ruficornis* group?] 252
vaga Panzer [synonym of *rufipes* Fabricius] 243
vagans Radoszkowski [incertae sedis] 258
valida Smith [*ruficornis* group] 253
vallesina Cockerell [*ruficornis* group] 253
varia Panzer [synonym of *fucata fucata* Panzer] 256
variabilis Lucas [incertae sedis] 258
varipes Pérez [synonym of *flavilabris* Morawitz] 247
vegana Cockerell [*vegana* group] 242
velardei Dusmet [synonym of *ibanezi* Dusmet] 248
velutina Swenk [*ruficornis* group] 253
ventralis Imhoff [synonym of *fulvicornis* Fabricius] 248
verecunda Cresson [*roberjeotiana* group] 243
vergiliana Pérez [synonym of *dira* Schmiedeknecht] 246
verna Schmiedeknecht [*ruficornis* group] 253
vernalis Morawitz [*ruficornis* group?] 253
vernonensis Cockerell [*ruficornis* group] 253
versicolor Panzer [incertae sedis] 258
versicolor Smith [synonym of *japonica* Smith] 255
vesparia (Gmelin) [synonym of *flava* Panzer?] 247
vespiformis (Forster) [see *vesparia* (Gmelin)] 247
vespiformis (Scopoli) [synonym of *flava* Panzer?] 247
vespoides (Schranck) [see *sexfasciata* Panzer] 255
vexator Cockerell [*ruficornis* group] 253
viburni Robertson [synonym of *obliterata* Cresson] 250
vicaroi Dusmet [synonym of *fenestrata fenestrata* Lepeletier] 247
vicina Cresson [*ruficornis* group] 253
vicinalis Cresson [*ruficornis* group] 253
victrix Cockerell [*vincta* group] 241
vidua Smith [synonym of *striata* Fabricius] 252
vierecki Cockerell [*vegana* group] 242
villipes [subspecies of *stigma* Fabricius] 240
villosa Thomson [*ruficornis* group] 253
vincta Say [*vincta* group] 241
vinnula Cresson [subspecies of *edwardsii* Cresson] 254
vitticollis Cresson [*vincta* group] 241
volatilis Smith [synonym of *maculata* Cresson] 249
vulpis Cockerell [*ruficornis* group] 253
wakasana Tsuneki [*ruficornis* group?] 253
waltoni Cockerell [*roberjeotiana* group] 243
washingtoni Cockerell [*ruficornis* group] 253
wheeleri Cockerell [*belfragei* group] 254
whiteheadi Eardley & Schwarz [*roberjeotiana* group?] 243
wickwari Meade-Waldo [*furva* group] 257
wisconsinensis Graenicher [*vegana* group] 242
wootonella Cockerell [*ruficornis* group] 253
wyomingensis Swenk [*ruficornis* group] 253
xanthaspis Cockerell [synonym of *limata* Cresson] 242
xanthidica [synonym of *japonica* Smith] 255
xanthogaster Cockerell [synonym of *belfragei* Cresson] 254
xantholepis Cockerell [*ruficornis* group] 253
xanthophila Cockerell [*roberjeotiana* group] 243
xanthopoda Schwarz [*trispinosa* group?] 256
xanthopus Friese [*vegana* group] 242
xanthosticta (Kirby) [synonym of *ferruginata* (Linnaeus)] 247
xanthura Cockerell [*ruficornis* group] 253
yagensis Tsuneki [*ruficornis* group?] 253
yanoi Tsuneki [*roberjeotiana* group?] 243
yarrowi Schwarz [*furva* group] 257
yasha Tsuneki [*ruficornis* group?] 253
yasuteyamana Tsuneki [*ruficornis* group?] 253
yunokawana Tsuneki [*ruficornis* group?] 253
zamoranica Cockerell [*vegana* group] 242
zebrata Cresson [*vincta* group] 241
zichyana Mocsáry [incertae sedis] 258
ziziae Swenk [*ruficornis* group] 253
zonalis Schwarz [*ruficornis* group] 253
zonata Panzer [*ruficornis* group] 253

ANNOUNCEMENT

The *University of Kansas Science Bulletin* (continuation of the *Kansas University Quarterly*) is an outlet for scholarly scientific investigations carried out at the University of Kansas or by University faculty and students. Since its inception, volumes of the *Bulletin* have been variously issued as single bound volumes, as two or three multi-paper parts or as series of individual papers. Issuance is at irregular intervals, with each volume prior to volume 50 approximately 1000 pages in length. Effective with volume 50, page size has been enlarged, reducing the length of each volume to about 750 pages.

The supply of all volumes of the *Kansas University Quarterly* is now exhausted. However, most volumes of the University of Kansas Science Bulletin are still available and are offered, in exchange for similar publications, to learned societies, colleges and universities and other institutions, or may be purchased at $30.00 per volume. Where some of these volumes were issued in parts, individual parts are priced at the rate of 3 cents per page. Current policy, initiated with volume 46, is to issue individual papers as published. Such separata may be purchased individually at the rate of 7 cents per page, with a minimum charge of $1.50 per separate. Subscriptions for forthcoming volumes may be entered at the rate of $30.00 per volume. All communications regarding exchanges, sales and subscriptions should be addressed to the Exchange Librarian, University of Kansas Libraries, Lawrence, Kansas 66045.

Individual papers for personal use by investigators are available for most recent and many older issues of the Bulletin. Such requests should be directed to the author or to the relevant Museum or Department of the University of Kansas.

The International Standard Serial Number of this publication is US ISSN 0022-8850.

Editor
Charles D. Michener

Editorial Board
Meredith Lane, *Chairman*
James S. Ashe
George W. Byers
Christopher Haufler
Norman A. Slade

THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. 55, No. 8, pp. 271-297 July 10, 1994

MCZ LIBRARY NOV 28 1994 HARVARD UNIVERSITY

A Revision of the New World *Trachusa*, Subgenera *Ulanthidium* and *Trachusomimus* (Hymenoptera: Megachilidae)

ROBBIN W. THORP[1] AND ROBERT W. BROOKS[2]

TABLE OF CONTENTS

Introduction 272
Acnowledgments 272
Genus *Trachusa* Panzer 272
Key to Species of the Subgenera *Trachusomimus* and *Ulanthidium* 274
Subgenus *Trachusomimus* Popov 276
T. perdita Cockerell, 277; *T. gummifera* Thorp, 277
Subgenus *Ulanthidium* Michener 279
Mitchelli Group 281
T. mitchelli (Michener), 281; *T. fulvopilosa* n. sp., 282
Manni Group 285
T. manni Crawford, 285; *T. alamosana* n. sp., 288; *T. notophila* n. sp., 289; *T. pueblana* n. sp., 291
Interdisciplinaris Group 291
T. interdisciplinaris (Peters), 295; *T. nigrifascies* n. sp., 295
Literature Cited 297

ABSTRACT

The New World subgenera of *Trachusa*, *Trachusomimus* and *Ulanthidium*, are revised. Each species is separated by a key, described, and pertinent morphological features are illustrated. Two species are recognized in *Trachusomimus*: *T. perdita* and *T. gummifera*. Eight species are recognized in three species groups of *Ulanthidium*: Mitchelli group, *T. mitchelli* (Michener), *T. fulvopilosa* n. sp.; Interdisciplinaris group, *T. interdisciplinaris* (Peters), *T. nigrifascies* n. sp.; Manni group, *T. manni* Crawford, *T. alamosana* n. sp., *T. notophila* n. sp. and *T. pueblana* n. sp. New World *Trachusa* s. l., except *Heteranthidium*, possess well-developed free volsellae.

[1] DEPARTMENT OF ENTOMOLOGY, UNIVERSITY OF CALIFORNIA, DAVIS, CALIFORNIA 95616, USA
[2] SNOW ENTOMOLOGICAL MUSEUM, UNIVERSITY OF KANSAS, LAWRENCE, KANSAS 66045-2119, USA

INTRODUCTION

The genus *Trachusa* (sensu Griswold and Michener, 1988) is diverse and consists of four subgenera in the New World. The most speciose is *Heteranthidium* Cockerell (11 species) found mainly in the United States (Brooks and Griswold, 1988), followed by *Ulanthidium* Michener (8 species) which is mainly Mexican, then *Trachusomimus* Popov (2 species) from California and *Legnanthidium* Griswold and Michener (1 species) from the southeastern United States. A revision of *Trachusomimus* and *Ulanthidium*, prompted by the recent re-evaluation of some anthidiine genera and subgenera (Griswold and Michener, 1988) and the discovery of five undescribed species, is presented here.

Michener (1941) reviewed and redescribed the genus and the three species then considered to be *Trachusa* and provided a key to separate them. Popov (1964) proposed a new genus, *Trachusomimus* for *Trachusa perdita* Cockerell based on a morphological and biological comparison with the Eurasian *T. byssina* (Panzer) and figured the genitalia of both species. Grigarick and Stange (1968) followed the recommendation of Thorp (1966) that *Trachusomimus* was not sufficiently different biologically from *Trachusa* to merit distinction as a genus and they treated *T. perdita* and *T. gummifera* Thorp as species of *Trachusa* s. lat. They recorded additional distribution data for the two species and gave a key separating them but did not figure the male genitalia.

The first characterizations of *Ulanthidium* (Michener, 1948; Michener and Ordway, 1964) when the taxon contained only *Trachusa mitchelli* (Michener), were significantly changed with the addition of two species. Peters (1972) added *U. (Olmecanthidium) interdisciplinaris* Peters and suggested that *Ulanthidium* and *Heteranthidium* differed little from *Trachusa*, especially in the broadened sense of Pasteels (1969). Griswold and Michener (1988) added *T. manni* Crawford and placed *Ulanthidium* as a subgenus of *Trachusa* emphasizing many new characters in addition to the characters given by Michener (1948).

Michener (1941) included presence of volsellae as a generic character based on males of *T. byssina* and *T. perdita*. Popov (1964) found that *Trachusa* s. str. and *Trachusomimus* have volsellae, but that *Legnanthidium* as *Heteranthidium ridingsii* (Cresson) does not. We find volsellae present in *Trachusa* s. str., *Legnanthidium*, *Trachusomimus* and *Ulanthidium* which is a plesiomorphy and rare among megachilids. The other American subgenus of *Trachusa*, *Heteranthidium*, lacks volsellae (Brooks and Griswold, 1988).

In the following discussion, descriptions and key we use the abbreviations T for metasomal tergum and S for metasomal sternum; thus S1 means the first metasomal sternum, etc. In the distributional data, F = female, M = male, P = with pollen. Institutional acronyms are given in the Acknowledgments.

ACKNOWLEDGMENTS

We appreciate the loan of material by H. V. Daly, University of California, Berkeley (UCB); G. E. Bohart and T. L. Griswold, Bee Biology and Systematics Laboratory, Utah State University, Logan (USU); J. Neff, Central Texas Melittological Institute, Austin (CTMI); R. R. Snelling, Natural History Museum of Los Angeles County (LACM); F. G. Werner, University of Arizona, Tucson (UAZ); Ricardo Ayala, Estación de Biología, Chamela, México (EBC); the Snow Entomological Museum, University of Kansas, Lawrence (SEM); and the R. M. Bohart Museum, University of California, Davis (RMBM). We are especially grateful for the opportunity to examine the type of *T. manni* loaned by R. G. McGinley of the National Museum of Natural History, Washington, D. C. and the type material of *U. interdisciplinaris* Peters loaned by J.-P. Kopelke of the Forschungsinstitut Senckenberg, Frankfurt. We thank C. D. Michener for graciously allowing us to use his manuscript description and drawings of *T. interdisciplinaris*. We thank Mary Ann Tenorio, California Academy of Sciences, San Francisco, for assistance in making the SEM photos and the University of Kansas Electronmicroscopy Facility for the use of its SEM.

RWB's part in this study was possible in part thanks to National Science Foundation grant BSR90-24723 (W. E. LaBerge, principal investigator) which enabled discovery of some of the new species and more complete data for those already known by RWB and other participants of the Programa Cooperativo sobre la Apifauna Mexicana (PCAM). Special thanks go to Dr. José Sarukhán (former Director of Instituto de Biología, UNAM), Chancellor of Universidad Nacional Autonomo de México, Dr. Jesús Guzman García of CONACYT (Mexico) and Ricardo Ayala, Estación de Biología, Chamela, who greatly facilitated the activities of PCAM.

Donna Stevens helped with inking some of the illustrations.

GENUS *TRACHUSA* PANZER

The following characters are given by Griswold and Michener (1988) to define the New World members of the genus *Trachusa*: Mandibles of male 3-toothed, of female with 3 or 4 teeth. Vertex well developed posteriorly, lateral ocellus therefore closer to eye than to posterior margin of vertex [equidistant in *T. (Heteranthidium) larreae* (Cockerell) and *T. (H.) bequaerti* (Schwarz)] and anterior margin of median ocellus closer to antennal bases than to posterior margin of vertex or equidistant. Spine of fore and mid tibia a blunt obtuse projection extending little if any beyond apical tibial margin, but extended anterobasally on tibial surface as carina, usually elevated to shoulder or angle anterobasally from angle at apical tibial margin. Hind basitarsus of female 2.5 to 3.5 times as long as broad and usually about as wide as tibia at basal third (thus wider than in most Anthidiini). T5 and T6 of female with apical margins linear, convex or acute medioapically (Figs. 1H-1K). Sterna of male usually without combs. T6 of male forming visible end of metasoma and its posterior margin slightly produced medially. T7 of male rather small, curled under, without projections or spines but diverse morphologically on apical margin (Figs. 1A-1G).

In addition to the generic characters, the subgenera *Trachusomimus* and *Ulanthidium* share a number of features, as follows: Body black with pale markings limited to face of male or sometimes absent; head broader than long; clypeus raised centrally, at least mediobasally; small tumid process between antennal bases; male flagellomere 1 longer than 2 and shorter than 2+3, 2 equal or subequal to 3; female flagellomere 1 subequal to 2+3; pronotal lobe without carina; mesepisternum without carina separating anterior and lat-

MCZ LIBRARY NOV 28 1991 HARVARD UNIVERSITY

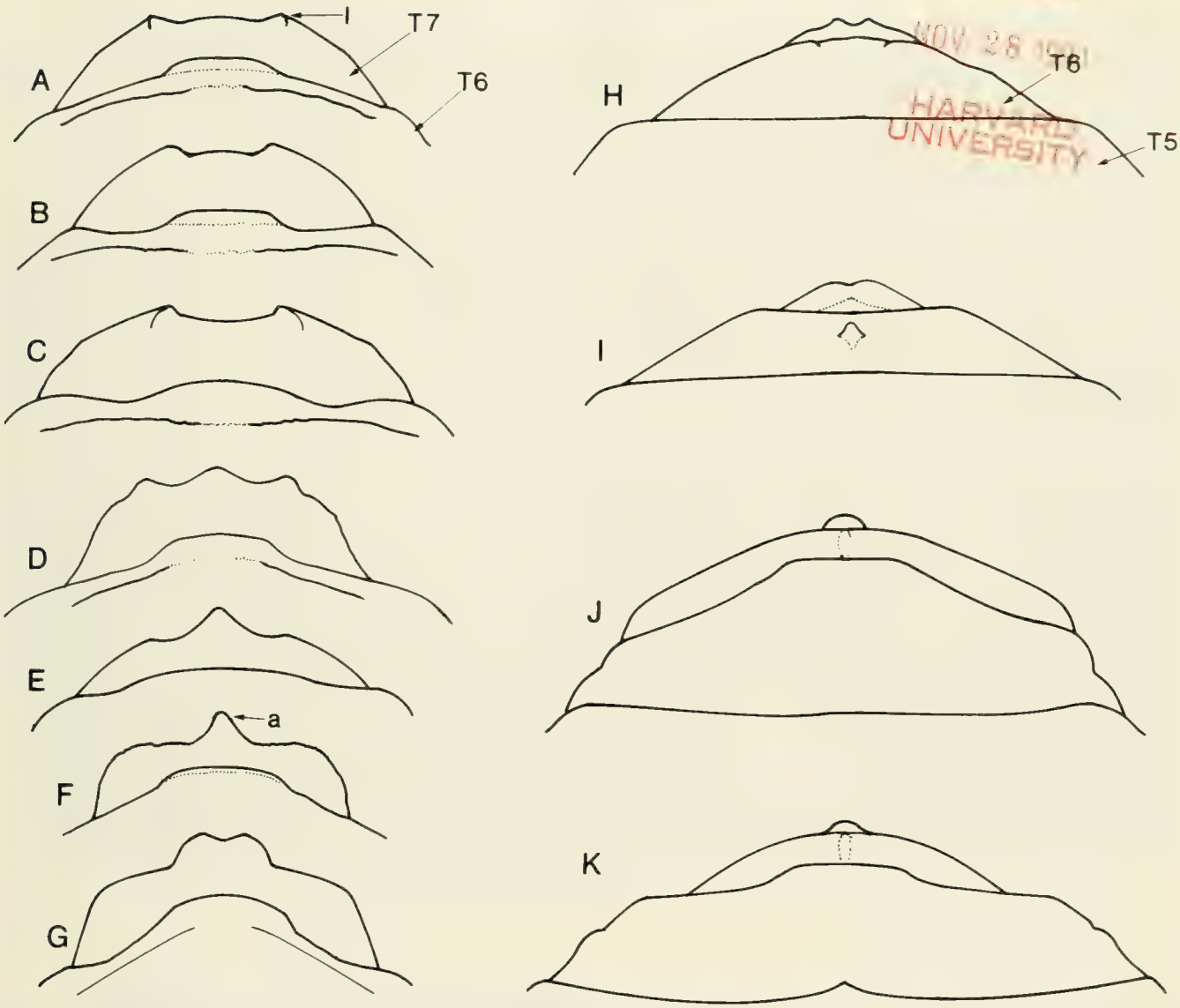


Fig. 1. Dorsal views of apices of male T6-T7 (A-G) and female T5-T6 (H-K) metasomas. All figures drawn to same scale: l = lateral protuberance, a = apical median projection. **A,** *Trachusa alamosana*; **B,** *T. manni*; **C,** *T. notophila*; **D,** *T. pueblana*; **E,** *T. interdisciplinaris*; **F,** *T. nigrifascies*; **G,** *T. mitchelli*; **H,** *T. alamosana*; **I,** *T. manni*; **J,** *T. interdisciplinaris*; **K,** *T. nigrifascies*.

eral surfaces; hair dense and plumose on hypostomal area and thorax; wings darkened with veins and stigma black; forewing with second recurrent vein meeting or slightly beyond second transverse cubital, basal vein meeting to slightly distad of cu-v; apical margins of terga strongly depressed and hidden by hairs; male T6 with apical flange and subapical ridge; volsellae of males well developed.

Pasteels (1969) expanded the generic concept of *Trachusa* to include several Old World "genera" as subgenera. He recognized that one genus could encompass considerable variability in what were traditionally thought to be generic characters (e.g., numbers of maxillary palpal segments and presence or absence of arolia). He also suggested that these characters might vary independently and that the "genus" *Ulanthidium* exemplified this.

Pasteels (1977) used biological characters to support his broadened concept of *Trachusa*, pointing out that *T.* (*Paraanthidium*) *interrupta* (Fabricius) builds nests of leaf strips and resin in the soil in a manner very similar to *T. byssina*. Similar nest construction characters were used by Griswold and Michener (1988) to support their broadened concept of *Trachusa* in North America.

Popov (1964) also used biological characteristics to supplement the morphological basis for his separation of *Trachusa* s. str. and *Trachusomimus* at the generic level. These, however, compared several detailed studies of *T. byssina*

and one study of active (incomplete) nests of *T. perdita* by Michener (1941). Subsequent studies of several nest sites of *T. perdita* and *T. gummifera* (Thorp unpublished) show that these differences do not hold. They are attributable to differences in local habitat or lack of specificity in host plants for pollen and leaf sources, species-specific differences in cocoon construction and interpretations based on unfinished nests of *T. perdita*. Indeed there are many similarities between the two subgenera including aggregated nests in soil, nest site habitats, leaf and resin brood cells, nest and cocoon architecture, leaf and resin gathering and carrying behavior, and vernal flight.

See Griswold and Michener (1988) for a key separating the four New World subgenera of *Trachusa*.

KEY TO SPECIES OF THE SUBGENERA *TRACHUSOMIMUS* AND *ULANTHIDIUM*

1. Arolia present (Figs. 3C,3D) (*Trachusomimus*) 2
—Arolia absent (Figs. 3E,3F) (*Ulanthidium*) 3
2. Face of male with pale markings not completely filling clypeus nor paraocular area below level of antennae, paraocular markings often absent, clypeal marking often reduced to lower one-third or less of clypeal area; T6 of male without median subapical protuberance; T7 of male with weak apicomedial emargination without enclosed flat brown plate (Fig. 6C); T6 of female without median subapical prominence but with sharp subapical medially weakly emarginate ridge (Fig. 6A); labial palpus with segment 3 longer than 4 (Fig. 2A) .....*gummifera*
—Face of male with well developed cream-colored markings, paraocular markings almost attaining lower margin of antennal socket, clypeus completely pale; T6 of male with median subapical protuberance (Fig. 4C); T7 of male with strong apicomedial emargination enclosing flat brown plate; T6 of female with median subapical prominence with median acute projection (Fig. 4A); labial palpus with segments 3 and 4 subequal in length .....*perdita*
3. Thirteen segments in antenna; seven exposed segments in metasoma (males) 4
—Twelve segments in antenna; six exposed segments in metasoma (females) 10
4. Face black; clypeus with long plumose hairs usually longer than length of first flagellomere; T7 with well developed pointed apical median projection, lateral protuberance absent (Figs. 1E, 1F) 5
—Face with pale markings; clypeus centrally with short, fine, simple hairs about as long as pedicel; T7 without apical median projection or, if present, then apical median projection bilobed or only attaining level of lateral protuberance (Figs. 1A-1D,1G) 6
5. T7 from dorsal aspect with narrowly rounded, apical median projection (Fig. 21D), ventral margin in apical view with deep medial emargination (Fig. 21C); S8 with lateral margins on apical half converging and straight without shoulders (Fig. 21G). .....*nigrifacies*
—T7 from dorsal aspect with apical median projection broader at base, more gradually narrowed apically (Figs. 20I,19C), apical view with ventral margin more or less straight (Fig. 20J); S8 with lateral margins on apical half converging but not straight, produced into shoulders (Fig. 20E) .....*interdisciplinaris*
6. T1-T5 not evenly covered but with distinct apical bands of hair pale to orange; T7 with pair of widely separated lateral protuberances (Figs. 1A-1D); maxillary palpus with four segments (Fig. 2A) 7
—T1-T5 evenly covered with fulvous to orange hair; T7 with rounded lateral shoulders and bilobed api-

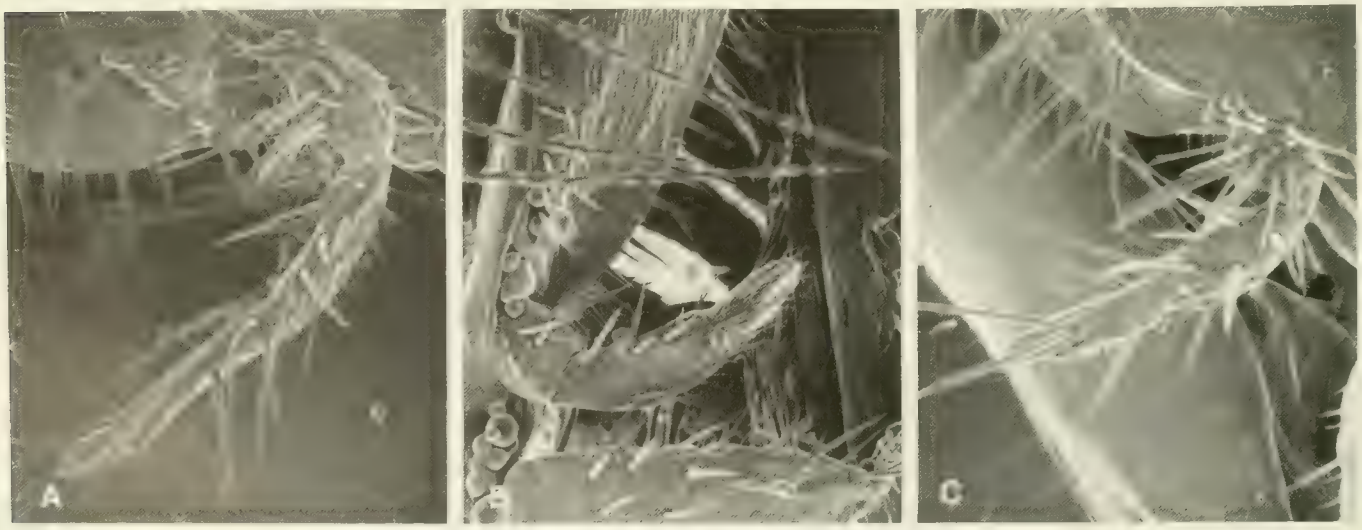


Fig. 2. Maxillary palpi. **A**, *Trachusa gummifera* with 4 segments; **B**, *T. mitchelli* with 3 segments; **C**, *T. alamosana* with 4 segments.

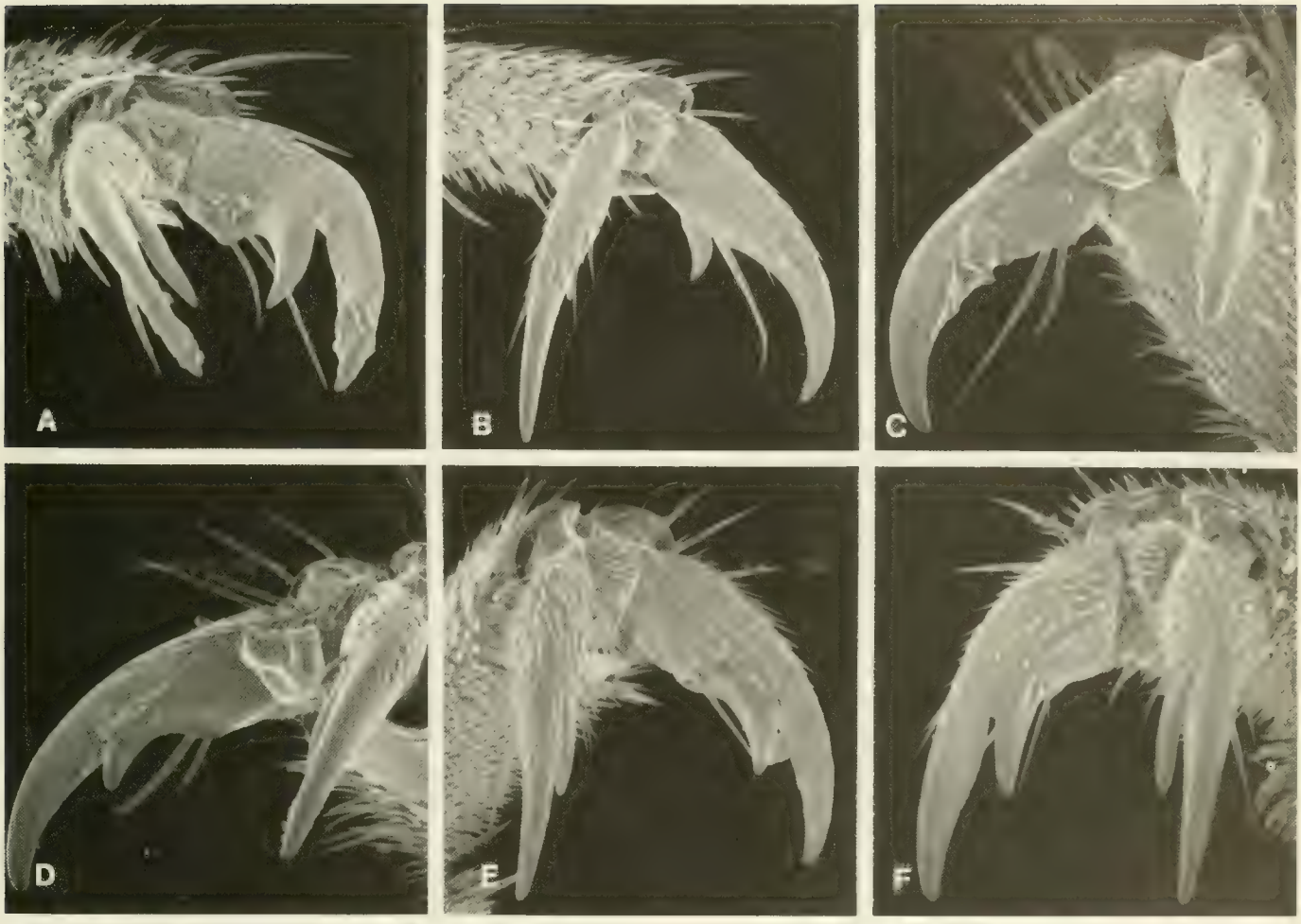


Fig. 3. Tarsal claws of females showing presence or absence of arolia, apicolateral views. **A,** *Anthidium maculosum* Cresson; **B,** *Megachile brevis* Say; **C,** *Trachusa gummifera* Thorp; **D,** *T. perdita* Cockerell; **E,** *T. alamosana* n. sp.; **F,** *T. mitchelli* (Michener).

cal median projection (Fig. 1G); maxillary palpus apparently three- segmented (Fig. 2B) ..... *mitchelli*

7. T7 without apical median projection, with pair of apical lateral protuberances (Figs. 1A-1C,11E); S8 with two apical lobes either closely approximated and with narrow, shallow emargination between lobes (Figs. 12E,16D) or with apical lobes widely separated and emargination between lobes about one-half as deep as length of disc (Fig. 14F) 8

—T7 with rounded apical median projection slightly exceeding lateral lobes (Figs. 1D,17A); S8 with two apical lobes widely separated and emargination between lobes about one-third as deep as length of disc (Fig. 18E) ..... *pueblana*

8. Pale paraocular mark not attaining lower margin of antennal socket; tegula black to dark brown, not translucent; apodeme of penis valve more or less straight (Figs. 12B,14B) 9

—Pale paraocular mark attaining level or about level of middle of antennal socket; tegula amber, translucent near margins; apodeme of penis valve curved strongly ventrad (Fig. 16B) ..... *notophila*

9. T7 with pair of strong, closely approximated lateral protuberances (Figs. 1B,11E); S8 narrowed on apical half with two narrowly separated apical lobes, spiculum long (Fig. 12E) ..... *manni*

—T7 with pair of weaker and more separated lateral protuberances (Fig. 1A); S8 wide on apical half with two widely separated apical lobes, spiculum short (Fig. 14F) ..... *alamosana*

10. Metasomal terga thickly covered with hair, no distinct apical bands of hair; maxillary palpus apparently three-segmented (Fig. 2B); hairs bristle-like near base of clypeus with stout bases but narrowing quickly and wavy at tips (Figs. 10A,10C) 11

—Metasomal terga not covered with hair but hair in distinct apical bands; maxillary palpus with four segments (Fig. 2C); hairs finer near base of clypeus, tips not wavy but straight or gently curved (Figs. 10B,10D) 12

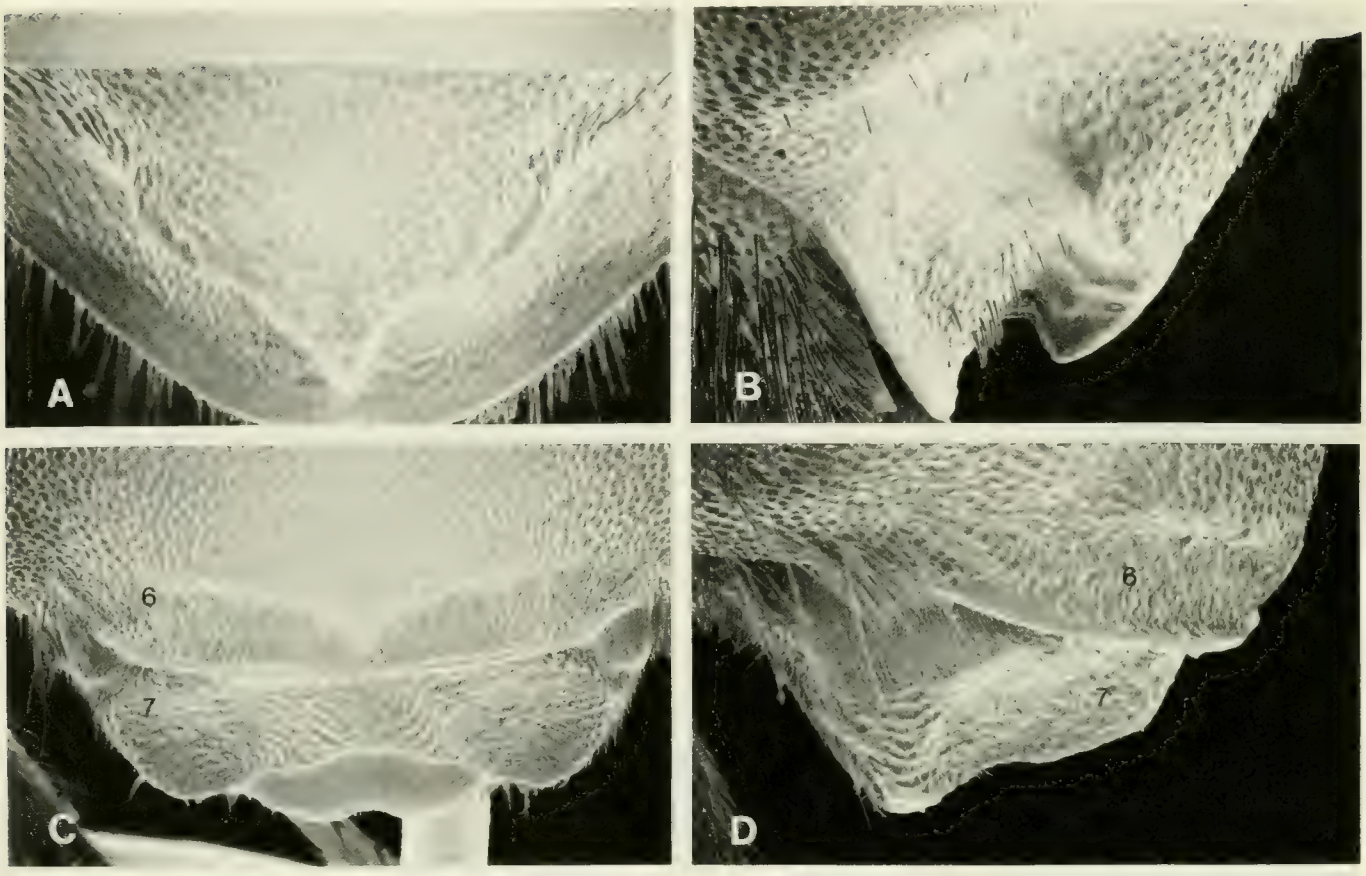


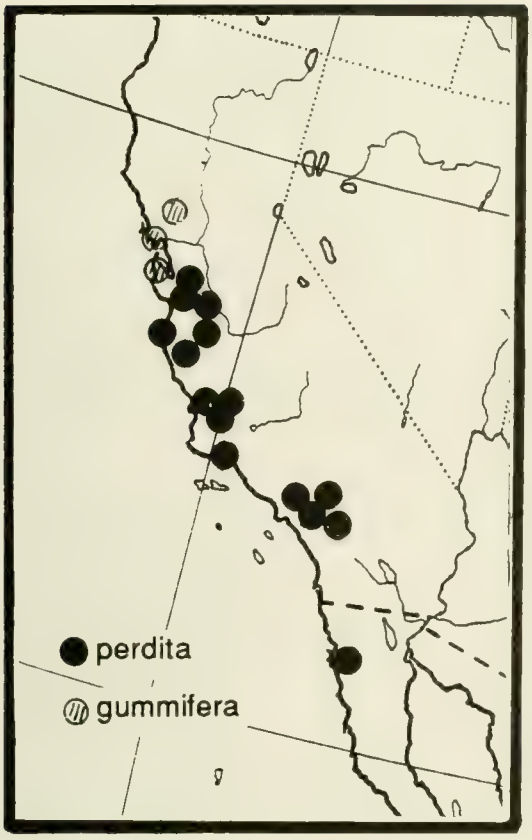
Fig. 4. *Trachusa perdita* metasomal apices. **A,B,** female T6, dorsal and side views; **C,D,** male T7, dorsal and side views. Side views have dorsal surfaces to the right.

11. Hair on head, thorax and T1-T3 black, T4-T6 reddish; clypeal margin pointed (Fig. 9F) . . . . . *.mitchelli*
—Hair on head, thorax and T1-T5 fulvous; clypeal margin broadly emarginate and with several teeth (Fig. 9G) . . . . . *.fulvopilosa*
12. Apical margin of T5 with wide median process (Figs. 1J, 1K); hairs on clypeus plumose and mostly much longer than length of flagellomere 1; T6 with strong subapical longitudinal ridge (Figs. 19A,19E) . .13
—Apical margin of T5 like preceeding terga, without any median process (Figs. 1H, 1I); hair on clypeus fine, simple and about as long as length of flagellomere 1; T6 without subapical longitudinal ridge (Fig. 13A) 14
13. Apical margin of T4 with median acute process (Fig. 1K) . . . . . *.nigrifascies*
—Apical margin of T4 without median acute process (Fig. 1J) . . . . . *interdisciplinaris*
14. T6 with strong median subapical protuberance (Fig. 1I) . . . . . *.manni*
—T6 without median protuberance (Fig. 1H) 15
15. T6 with broad median longitudinal groove covered by thick patch of white hair which completely covers surface (Fig. 15A); T3-T5 with strongly protruding dorsal convexities at right angles to marginal zones (Fig. 16G) . . . . . *.notophila*
—T6 with median longitudinal zone flat to convex and sparsely covered by white hair not obscuring surface (Fig. 13A); T3-T5 with dorsal convexites almost in same plane as marginal zones (Fig. 14H) . . .*alamosana*

SUBGENUS *TRACHUSOMIMUS* POPOV

Trachusomimus Popov, 1964:406. Type species: *Trachusa perdita* Cockerell, 1904, by original designation.

MALE: Creamy yellow markings limited to face; inner orbits converging slightly below; ocellocular distance equal to (posterior) interocellar distance; middle ocellar diameter slightly greater than distance between ocelli; clypeal margin with 7-8 apical denticles between which arise tufts of light brown hair; mandible with teeth nearly equidistant; maxillary palpus as long as maximum width of galea, 4-segmented (Fig. 2A). Pronotal lobe not carinate, with weak vertically directed ridge basally; scutellum not depressed along midline, not biconvex; arolia present (Figs. 3C,3D). T6 with margin convex and somewhat produced, with truncate apex nearly as broad as T7 (Figs. 4C,6C), a preapical ridge [stronger in *T. gummifera* than in *T. perdita* (Figs. 4C,6C)] in front of transverse preapical cavity; T7 with shallow median apical emargination, a preapical



Map 1. The distribution of species of *Trachusomimus*.

ridge (the apparent tergal apex in *T. gummifera*) V-shaped medially, the V open posteriorly and enclosing a bare area (Figs. 4C,6C); S6 with triangular median apical projection (Figs. 5H,7G); S7 broad with deep, rounded midapical emargination; S8 with body hairy, somewhat broader than long, apex with median lobe itself weakly bilobed (Figs. 5E,7C); gonostylus with apex slightly broadened and bidentate, but without cleft separating small lateral lobe (Figs. 5A,5B,7A,7B). Pubescence white except yellow-buff to reddish on thoracic dorsum; S2-S5 with apical bands of long, sparse hair; hair of T1-T5 other than white marginal bands erect, sparse, moderately long; hair of T6-T7 appressed and short. Punctation moderately coarse and dense throughout except for shagreened lower part of propodeal triangle, punctures about 1 diameter apart or less mediolongitudinally on clypeus, elsewhere contiguous on thoracic dorsum.

FEMALE: Agrees with description of male except for usual sexual characters; face black; pubescence of clypeus short and white; inner orbits not converging below, parallel to slightly diverging; ocellar diameter equal to distance between ocelli; T6 of female with strong preapical ridge [only medially in *T. perdita* (Fig. 4A), but complete in *T. gummifera* (Fig. 6A)], behind which is a transverse concavity before apical flange; punctation of clypeus denser, punctures more or less contiguous and coarse; median half of T6 densely covered with silvery white appressed hair.

Trachusa perdita Cockerell
Figs. 3D,4A-4D,5A-5H, Map 1

Trachusa perdita Cockerell, 1904, p. 159.

MALE: Length 13 mm; forewing length 9.5 mm (7.5 from tegula to tip cell M). Clypeus and paraocular areas below level of antennae creamy. Pubescence white except yellow-buff tinge on thoracic dorsum; hair of T6-T7 appressed and short. Punctures moderately coarse and dense throughout, about 1 diameter apart mediolongitudinally on clypeus to less than 1 diameter apart elsewhere, contiguous on thoracic dorsum. Labial palpus with segments 3 and 4 subequal in length. T6 with subapical ridge bending medioapically as acute V nearly reaching margin (Figs. 4C,4D); T7 with flat, translucent apical shelf filling median subapical emargination (Fig. 4C); S6 with pair of ventrally directed teeth medioapically (Fig. 5H); S8 short, more or less narrow, apical projection shallowly emarginate with two subapical lateral protuberances at widest part (Fig. 5E); penis valve not tapering abruptly beyond bend to acute apex, rather finger-like (Figs. 5A,5B).

FEMALE: Length 12 mm; forewing length 8.5 mm [7 mm from tip cell M to tegula]. Agrees with description of male except sex limited characters; hair appressed and sparse on T5; scopa golden; punctation of clypeus denser, more or less contiguous and coarse; T6 with subapical V-shaped carina (Figs. 4A,4B).

Distribution: *Trachusa perdita* occurs in the coastal and transverse ranges of California from Mt. Diablo to Santo Tomás, Baja California (Map 1). Cockerell (1904) gave the type locality as Tehachapi, Kern County, California. We have examined 101 males and 200 females. In addition to those listed in Grigarick and Stange (1968) we have seen specimens from the following localities: **Baja California**: Santo Tomás. **California**: *Contra Costa Co.*: Mt. Diablo. *Monterey Co.*: Arroyo Seco; Carmel. *San Benito Co.*: Paicenes, 12 mi. (19.3 km) S. *San Bernardino Co.*: Deep Creek Public Camp; San Bernardino Mountains, Seely Flat. *San Luis Obispo Co.*: Creston, 2.5 and 6 mi. (4 and 9.6 km) S. *Santa Clara Co.*: Alum Rock Park; Coe Park; San Jose. *Stanislaus Co.*: Del Puerto Canyon, Frank Raines Park.

In addition to those listed by Grigarick and Stange (1968), nest site collections are noted on labels of series of specimens from: *Contra Costa Co.*: Mt. Diablo. *Los Angeles Co.*: Tanbark Flat. *Riverside Co.*: Lake Mathews Rd., 1 mi. (1.6 km) E. Hwy 71. *San Luis Obispo Co.*: Santa Margarita, 5 mi. (8 km) NE; Simmler, 10 mi. (16.1 km) W.

Flight records for both sexes range from 14 April to 18 July with 50% of the records for males in the later half of May and for females in the early half of May.

Flower records include: *Brodiaea* 2F, *B. lutea* 1M, 1F; *Calochortus* 1F(P); *Calystegia* 1M; *Clarkia* 2M, 3F, *C. cylindrica* 9M, 18F(P), *C. purpurea* 1F(P); *C. speciosa* 2F(P); *Collinsia* 6F(2P); *Eriodictyon* 1M, 3F; *Eriophylum confertiflorum* 1F; *Layia platyglossa* var. *breviseta* 1F; *Lupinus nanus* 3M, 39F; *Malacothrix californica* 1F; *Penstemon antirrhinoides* 10M, 6F; *Salvia carduacea* 1M, *S. columbariae* 2F. These records as well as examinations of pollen loads on females collected at nest sites and pollen in brood cells (Thorp, unpublished) demonstrate that *T. perdita* is polylectic.

Trachusa gummifera Thorp
Figs. 2A,3C,6A-6D,7A-7G, Map 1

Trachusa gummifera Thorp, 1963, p. 56.

MALE: Length 13 mm; forewing length 9.5 mm [8 from tegula to tip of cell M]. Yellow maculation not completely occupying entire clypeus, often restricted to lower third and extending upwards medially with carmel border above. Pubescence red-brown on vertex, thoracic dorsum, laterally just below tegulae and tergal discs; hair bands on T1-T3 medially interrupted. Punctation rather fine and dense throughout. Labial palpus with segment 3 longer than 4. T6 with rounded transverse subapical carina, only slightly produced apicad medially (Fig. 6C); T7 narrowly emarginate apicomedially, not enclosing flat brown plate (Fig. 6C); S6 with obtuse ventral projection apically (Fig. 7G); S8 apex with two well separated narrow processes, depth of cleft between processes

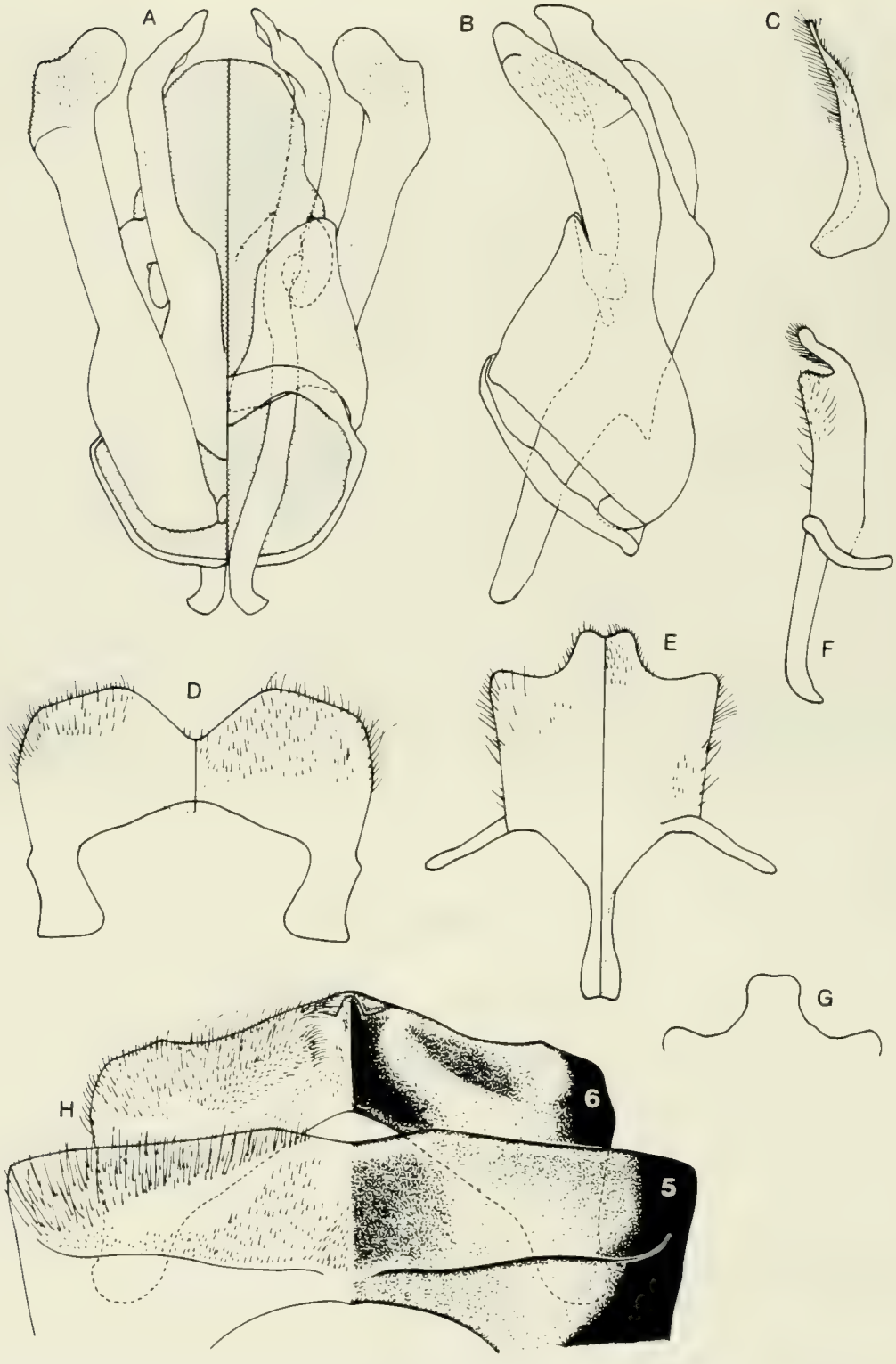


Fig. 5. Male terminalia of *Trachusa perdita*. In divided views (A, D, E) right side is ventral and left is dorsal. All figures drawn to same scale. A,B,D-F,H drawn from specimen from 12 mi (19.3 km) N. E. Pozo, Calif., C,G drawn from specimen from Mt. Diablo, Calif. **A,B,** genital capsule, dorsoventral and side views; **C,D,** S7, side and dorsoventral views; **E-G,** S8, dorsoventral, side and apical fourth views; **H,** S5 and S6, ventral view.

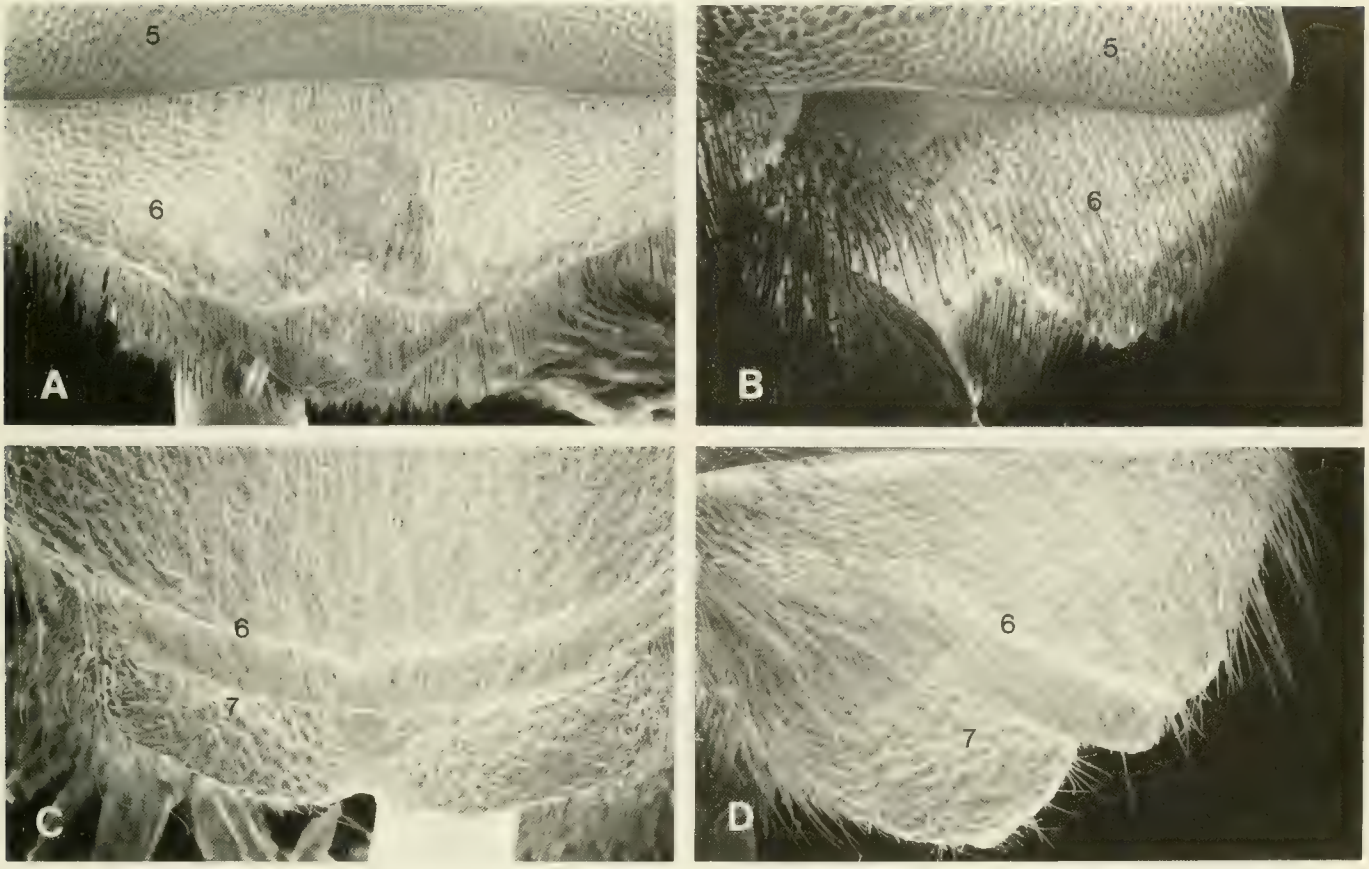


Fig. 6. *Trachusa gummifera* metasomal apices. **A,B,** female T6, dorsal and side views; **C,D,** male T7, dorsal and side views; side views have dorsal surfaces to right.

about 1/5 length of disc (Fig. 7C); penis valve tapering rapidly from bend to acute apex (Figs. 7A,7B).

FEMALE: Length 13 mm; forewing length 9.5 mm [8 mm from tegula to tip M cell]. Agrees with description of male except for sex limited characters; scopa yellow-brown; apical margin of T5 slightly emarginate; T6 with subapical carina emarginate medially (Fig. 6A).

Distribution: *Trachusa gummifera* is known only in the coast ranges from San Francisco to Napa County, California (Map 1). In addition to the specimens recorded by Thorp (1963) we have seen 9 females from *Napa Co.*: 1F, Mt. Veeder, 10 mi. (16.1 km) NW Napa, on *Pickeringia*, 5 June 1978, 6F, 5 June 1979 and 2F, 10 June 1980.

Flight records for the 5 males and 48 females range from 30 May to 11 June for males and 30 May to 30 June for females.

Although the only flower record on specimens is *Pickeringia* (Dobson, 1993), examinations of pollen loads on females and pollen in brood cells from Carson Ridge (Thorp, unpublished) indicate that this species is polylectic.

SUBGENUS *ULANTHIDIUM* MICHENER

Ulanthidium Michener, 1948:13. Type species: *Ulanthidium mitchelli* Michener, 1948, by original designation.
Olmecanthidium Peters, 1972:377. Type species: *Ulanthidium interdisciplinaris* Peters, 1972, by original designation.

MALE: Yellow markings absent or limited to face. Inner orbits converging below; ocellocular distance less to greater than (posterior) interocellar distance; middle ocellar diameter greater than distance between ocelli; clypeus with 4-8 apical denticles between which arise tufts of hair (Fig. 10B); mandible with teeth equidistant or middle tooth closer to outer than to inner tooth; maxillary palpus not longer than width of galea, 4-segmented with 4th segment small and not clearly separated from 3rd (Fig. 2C), or apparently 3-segmented (Fig. 2B); pronotal lobe not carinate; arolia absent as in *Anthidium* and *Megachile* (Figs. 3A,3B,3E,3F). T6 with margin produced and subtruncate medially [feebly so in *T. interdisciplinaris* (Figs. 19C,19D)], apex not as broad as T7 (Fig. 8C), with preapical ridge laterally; T7 with narrow median apical projection, usually bilobed, sometimes trilobed or simple; S6 with triangular, rounded, or bilobed median apical projection; S7 short, transverse, with apical sublateral lobe (Figs. 20H,21E) or in *T. mitchelli* with strong apical submedian lobe on each side (Fig. 9E). S8 with body about as long as broad with two apical hairy lobes (Figs. 9E,12E) or teeth, or a single median lobe in *T. interdisciplinaris* (Fig. 20E). Gonostylus with apex slightly broadened and bidentate, with cleft separating small lateral lobe (Fig. 9B). Punctation moderately fine and dense throughout except absent on shagreened lower part of propodeal triangle, and sparse on shiny, lower portion of mesepisternum; extreme lower margin of supraclypeal area dull.

FEMALE: Agrees with description of male except for sex limited characters; clypeus with sparse short simple hairs, sometimes hooked at tips (Fig. 10C); T6 with longitudinal median ridge (Fig. 8A), preapical ridge interrupted medially or feebly developed

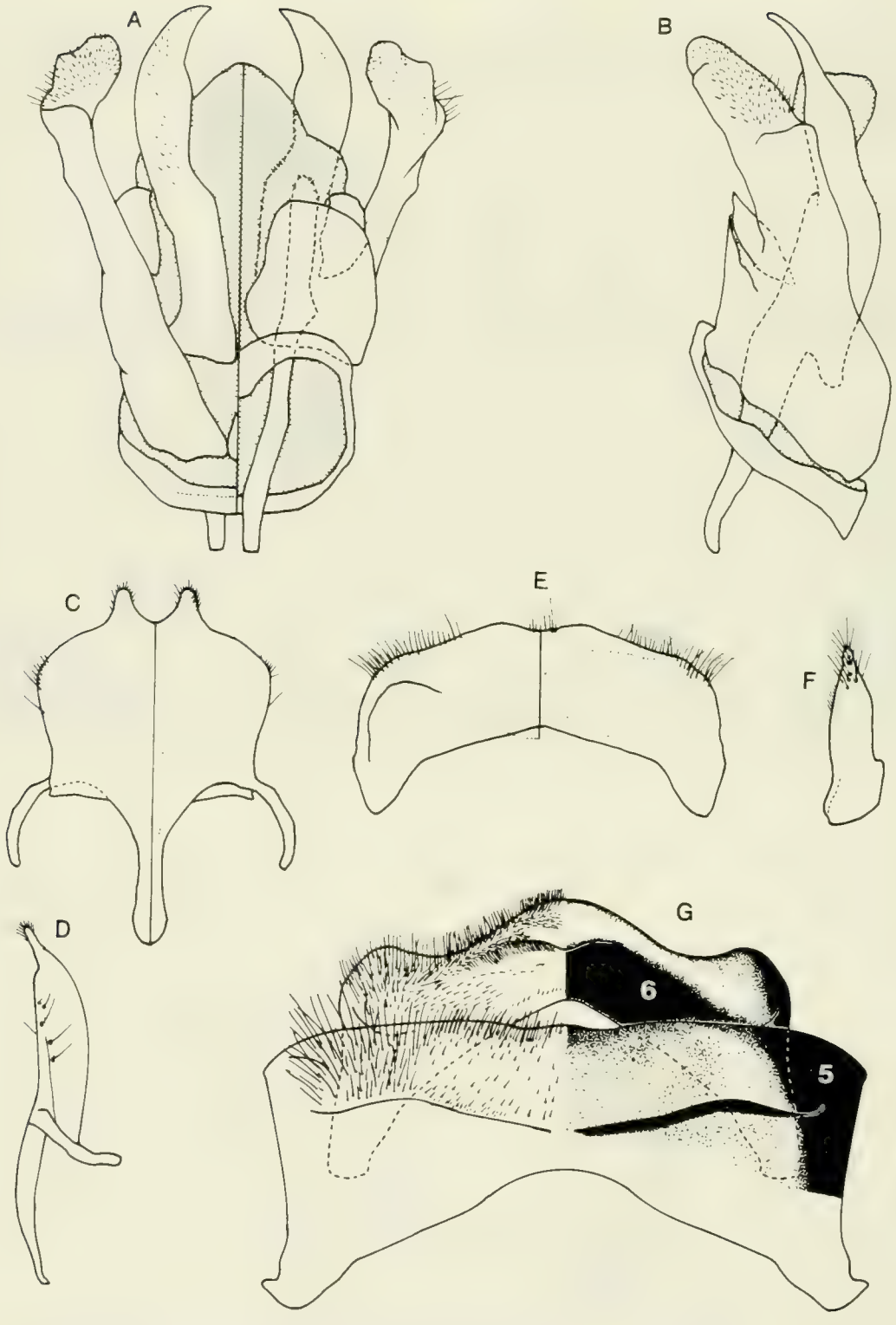


Fig. 7. Male terminalia of *Trachusa gummifera*. In divided views (A,C,E) right side is ventral and left is dorsal. All figures drawn to same scale. **A,B,** genital capsule, dorsoventral and side views; **C,D,** S8, dorsoventral and side views; **E,F,** S7, dorsoventral and side views; **G,** S5 and S6, ventral view.

Map 2. The distribution of species in the Mitchelli Group.

and present only laterally in *T. mitchelli*, absent in *T. interdisciplinaris* (Figs. 19A,19B); middle ocellar diameter greater than distance between ocelli in Manni Group only.

Ulanthidium is a diverse assemblage of autumnal species. In addition to its subgeneric morphological features, each of the three groups has its distinct apomorphies. The most distinctive is the Mitchelli Group originally assigned to *Ulanthidium*. If additional characteristics confirm the distinctness of the Mitchelli Group from other *Ulanthidium*, the subgeneric name *Olmecanthidium* Peters could be used for the Interdisciplinaris and Manni Groups.

Mitchelli Group

The two species, *T. mitchelli* and *T. fulvopilosa*, which comprise the Mitchelli Group, are characterized as follows: Hair evenly covering terga, not forming apical hair bands on T1-T5; clypeus with short, fine, simple hairs (excluding hair on apical margin), about as long as the pedicel, with hooked or wavy tips in females (Figs. 10A,10C); T7 of male with a bifurcate apical median projection (Figs. 1G,8C); face of male with pale markings; and maxillary palpus apparently 3-segmented (Fig. 2B).

Since the male of *fulvopilosa* is unknown, group characters listed below are primarily those shared with females or parallel to group characters in other *Trachusa*.

MALE: Clypeus and paraocular areas below level of antennae ivory; ocellocular distance less than (posterior) interocellar distance. Clypeus flat laterally, with median longitudinal convexity; mandible broad with middle tooth closer to outer than to inner tooth (Fig. 9F); maxillary palpus apparently 3-segmented (Fig. 2B). Second recurrent vein interstitial with second transverse cubital; wings heavily stained dark brown; mesepisternum with lower half shiny and sparsely punctate. T1-T5 with margins depressed, hidden by hairs, but without apical hair bands. Pubescence dense throughout, largely hiding surfaces of metasomal terga; hair of metasomal terga long, erect, plumose and concolorous on discs and depressed margins.

FEMALE: Agrees with description of male except for sex limited characters; face black; sparse short simple black hairs hooked at tips on clypeus and above to ocelli (Figs. 10A,10C); hair short, appressed, coppery on T6; eyes only slightly converging below (Figs. 9F,9G). Mesepisternum with only lower 1/4 shiny and impunctate.

Trachusa mitchelli (Michener)

Figs. 1G,2B,3F,8A-8D,9A-9F,10A,10C, Map 2

Ulanthidium mitchelli Michener, 1948, p. 13.

This species (Michener, 1948) was initially based on the female alone. A male was tentatively associated with this remarkable female and described (Michener and Ordway, 1964). We concur that the sexes of this dimorphic species are probably properly associated. We note corrections or different interpretations in Figures 23, 26, and 27 of Michener and Ordway (1964). In their Fig. 23 in the dorsal view of the penis value, the lobe on the median section is interpreted by us differently (see our Fig. 9B). The apical emargination shown in their Fig. 26 of S8 is shown differently (see our Fig. 9D) as well as the spiculum is trilobed and not simple as shown in their Fig. 26. Their Fig. 27 was drawn from a damaged, incomplete S7 but is redrawn from a complete sternum here (see our Fig. 9E).

MALE: Length 13 mm; forewing length 10 mm [8 from tegula to tip cell M]. Pubescence fulvous above from vertex of head to T5, white on lower gena and thoracic pleura, legs basally and on outer surfaces distally, and on sterna; hairs short, sparse, simple, straw yellow on clypeus and not hooked at tips as in female; short, simple, sparse, decumbent, coppery hairs on T6-T7; S2-S5 with loose, white, apical hair bands, hairs long laterally on S2-S5, dense and more plumose medially on S4, short dense and coppery medially on S5-S6. Punctures more than 1 diameter apart on clypeus, finest on upper face and genae, contiguous on thoracic dorsum, separated by less than 1 diameter elsewhere. Ocellar diameter about equal to distance between ocelli; clypeus more or less extended and pointed medioapically, with translucent brown apical margin, margin thicker and darker than in other species, with 4 denticles between which arise tufts of light brown hair; T6 with median apical flange about half as broad as width of T7 (Fig. 8C); T7 with weak median longitudinal carina, medioapical bilobed projection and weak lateral shoulders (Fig. 8C); S6 with pair of tumid subapical processes ventrally and thin bilobed process apically; S8 with apical lobes widely separated and tapering to squarish shoulders, cleft about third length of disc (Fig. 9D); penis valve with narrow subapical neck curved to obliquely truncate apex pointed ventrally (Figs. 9A,9B).

FEMALE: Length 13 mm; forewing length 10 mm [8 mm from tegula to tip cell M]. Agrees with description of male except for sex limited characters; pubescence black from head through T3, brick red on T4 and T5; scopa black. Ocellar diameter less than distance between ocelli; clypeal margin medioapically pointed, long black hair clump emerging beneath and projecting beyond apex; T5 with apical margin sinuate, projecting rearward only slightly medially; T6 with longitudinal median ridge highest basally, apical flange produced as narrow, rounded median projection but elsewhere absent so that except medially there is no depressed margin or preapical concavity (Fig. 8A).

Distribution: *Trachusa mitchelli* occurs in southwestern México from Jalisco to Oaxaca (Map 2). Michener (1941) described the species based on a female from Tecolotlán, Jalisco, México. Michener and Ordway (1964) described the male from Chapala, Jalisco,

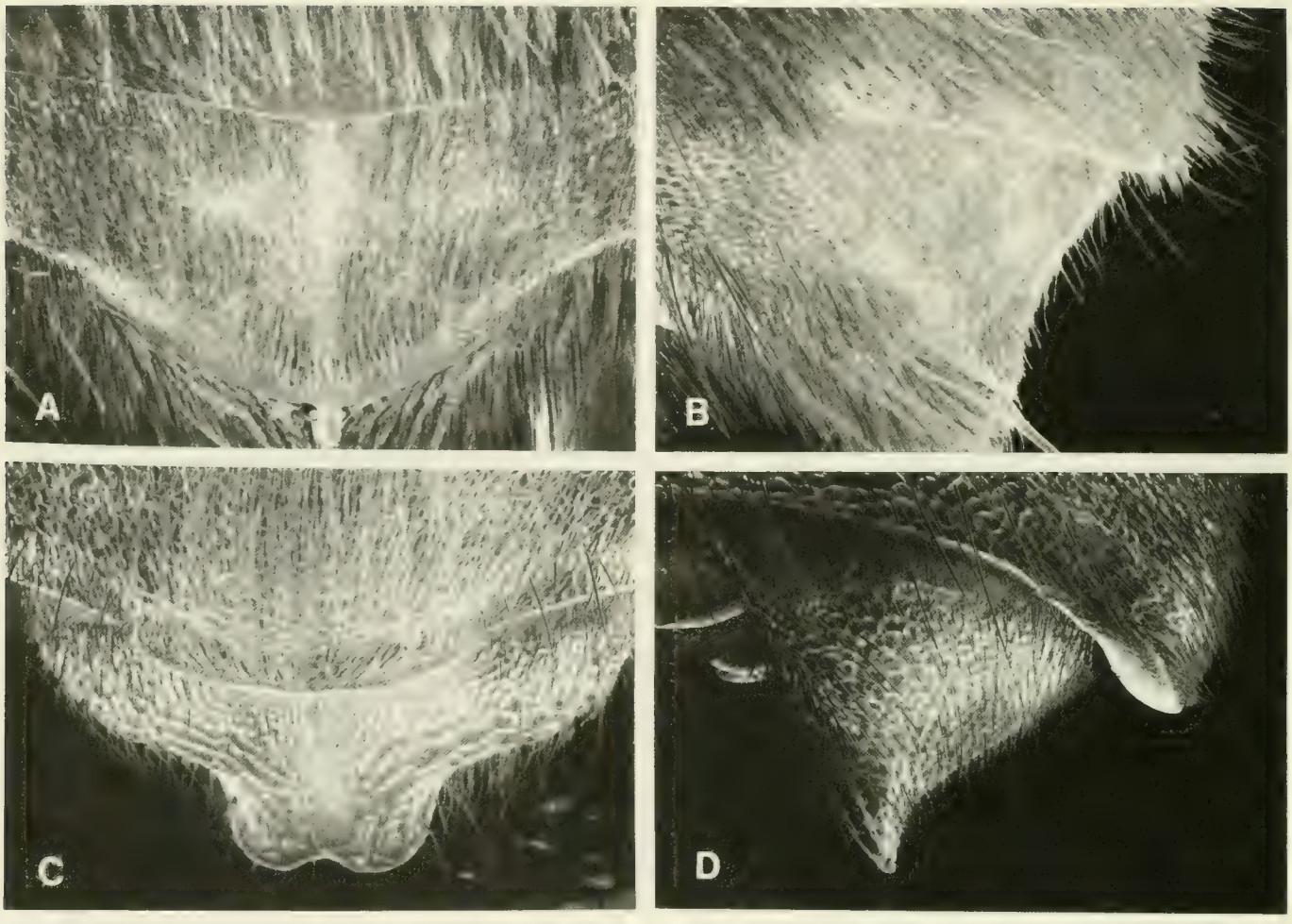


Fig. 8. *Trachusa mitchelli* metasomal apices. **A,B,** female T6, dorsal and side views; **C,D,** male T7, dorsal and side views; side views have dorsal surfaces to the right.

México. Additional specimen data include: **Hidalgo:** 2M, 4 km N. Metzquititlán, 1580m, 11 November 1991, R. Ayala, T. Griswold (EBC and USU). **Jalisco**: 1F, Mts. N. Ajijic, Scrub forest, 6500' (1981m), 3 October 1964, and 1F, 7500' (2286m), 20 September 1964, W. L. Nutting & sons (SEM, UAZ); 1F, Guadalajara, 47 mi. (75.6 km) SE., 12 September 1972, J. M. Poff and W. J. Hanson (USU); 1M, Rt. 15, 4 mi. (6.4km) E. Soyatlan, 1500m, 16 October 1975, J. L. Neff (CTMI). **Michoacán**: 1M, 40 mi. (64.3km) W. Morelia, 6800' (2072m), 22 September 1957, H. A. Scullen (USU); 2M,1F, 4 mi. (6.4km) E. Pátzcuaro, 13 September 1972, W. Hanson & J. Poff (USU); 2M, 7.7 km NE. Pátzcuaro, 2088m, 23 September 1976, on *Salvia polystacha*, C. D. George & R. R. Snelling (LACM); 1M, Zintzuntán, N. Pátzcuaro, 2100m, 26 October 1987, T. Griswold (USU), 3M, L. Godínez (SEM). **Oaxaca**: 2M, Hwy 125, 2 mi. (3.2km) S. Puebla-Oaxaca state line, 6000' (1829m), 6 October 1975, J. Powell, J. Chemsak, T. Eichlin, T. Friedlander (UCB). **Puebla**: 1F, 6.9 km S. Izúcar de Matamoros, 1250m, 17 September 1976, on *Solanum rostratum*, C. D. George & R. R. Snelling (LACM).

Trachusa fulvopilosa new species

Figs. 9G,11A,11B, Map 2

MALE: Unknown.

FEMALE: Length 13 mm; forewing length 10 mm (8 mm from tegula to tip cell M). Pubescence fulvous on vertex of head, dorsum of thorax and T1-T5, white on rest of head, thoracic pleura, leg bases, T6, laterally on T2-T5, S1 and base of S2, rust-brown on rest of sterna, outer surfaces of tibiae and tarsi. Punctures coarse and mostly sparse (ca 1 diameter apart) on clypeus, coarser and more dense on paraocular and supraclypeal areas, finest on upper face and genae, contiguous on thoracic dorsum, separated by less than 1 diameter elsewhere; clypeus with slightly incurved margin (Fig. 9G); T6 (Figs. 11A,11B) not as carinate as in *T. mitchelli* (Figs. 8A,8B), but more tumid mediobasally.

Type material: The holotype female of *T. fulvopilosa* is from México: **Chihuahua**: Temoris, 2 mi. (3.2km) N., 8 September 1969, T. A. Sears, R. C. Gardner, C. S. Glaser (RMBM).

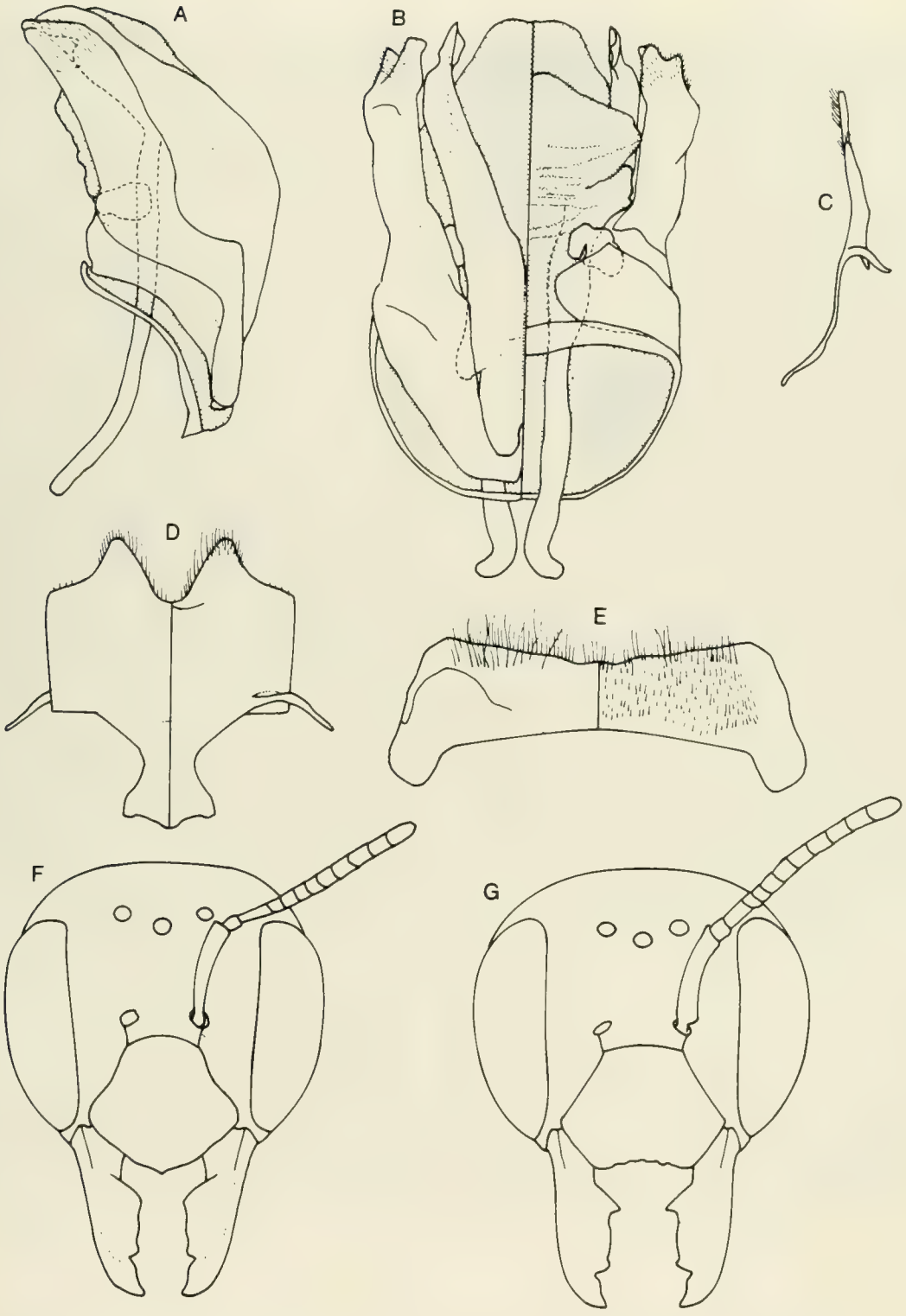


Fig. 9. Male terminalia and female heads of Mitchelli group. In divided views (B,D,E) right side is ventral and left is dorsal. Heads not drawn to same scale as terminalia. A-F, *Trachusa mitchelli*, G, *T. fulvopilosa*. **A,B,** genital capsule, side and dorsoventral views; **C,D,** S8, side and dorsoventral views; **E,** S7, dorsoventral view; **F,G,** heads, front views.

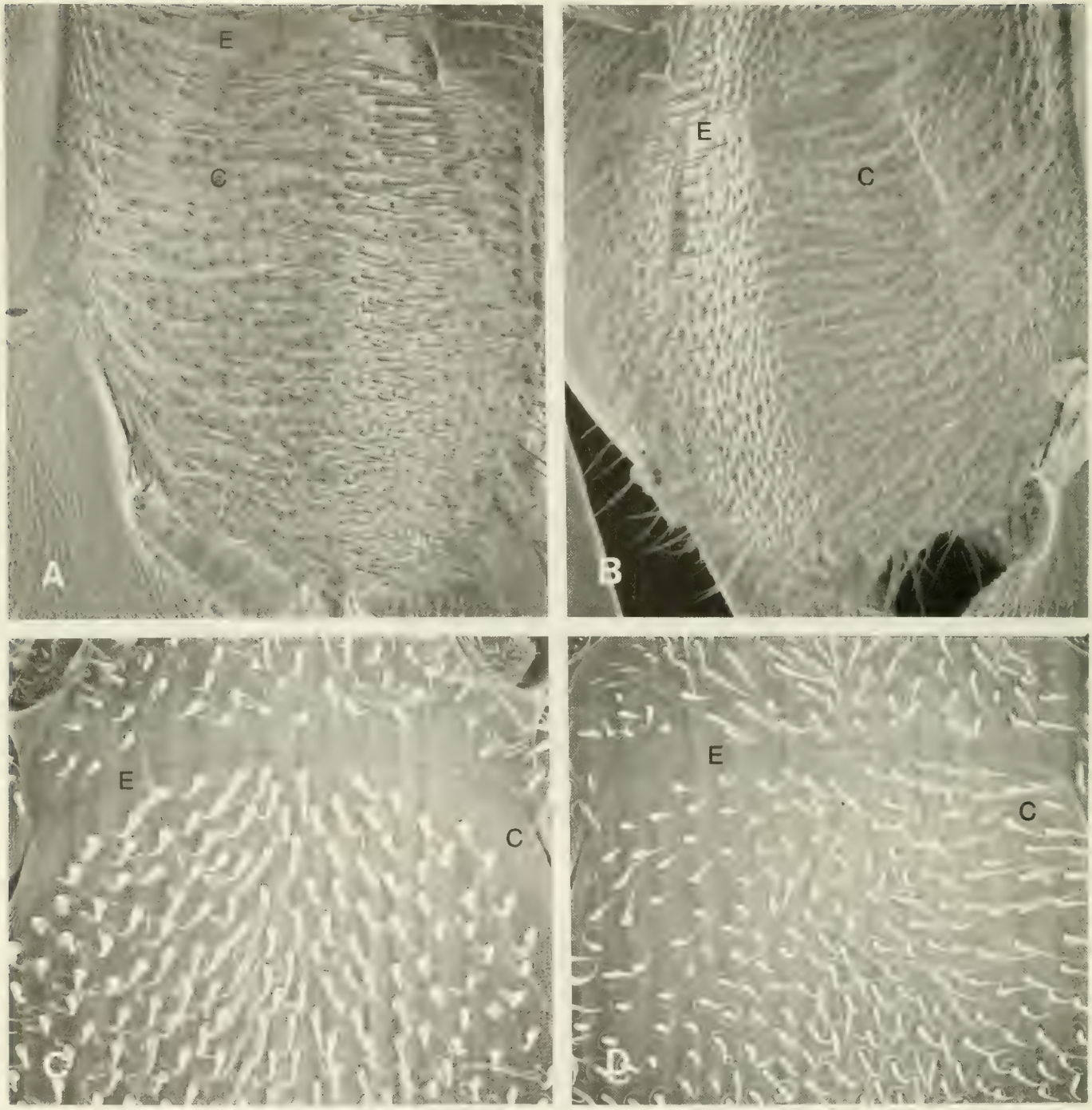


Fig. 10. Female clypei of *Ulanthidium*. e – epistomal suture; c – clypeus. A,C, *Trachusa mitchelli* and B,D, *T. alamosana*. **A,B,** fronto-lateral views, A, front toward right; B, front toward left; **C,D,** front views.

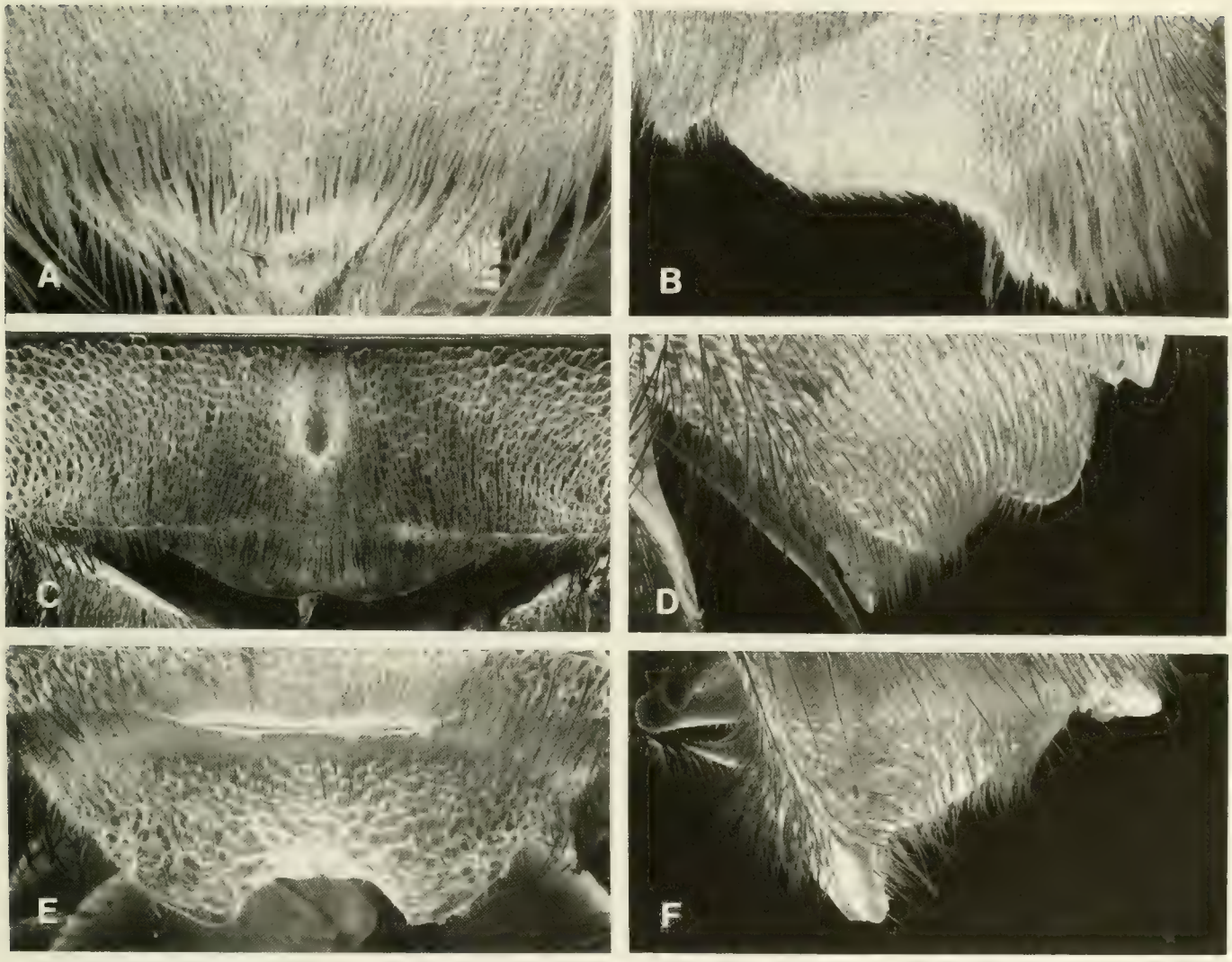


Fig. 11. Metasomal apices. **A,B,** *Trachusa fulvopilosa*, female T6, dorsal and lateral views; **C,D,** *T. manni* female T6 dorsal and lateral views; **E,F,** *T. manni* male T6 and T7, dorsal and lateral views. In B, dorsal surface is to left; D and F, to right.

Manni Group

The four species, *T. manni, T. alamosana, T. notophila* and *T. pueblana*, that comprise this group look similar to species of *Trachusomimus*. The presence in the male of apical hair bands on T1-T5 and in the female of fine, simple clypeal hairs, about as long as flagellomere 1 (Figs. 10B,10D) is diagnostic. Other characteristics include the face of the male with pale markings, apical margin of T5 of the female normal, like preceding terga, and T6 in the female without a subapical median longitudinal ridge.

MALE: Clypeus and paraocular areas below level of antennae yellow. Pubescence moderately dense basolaterally on T7 except median apical nearly bare area, and forming dense pale apical bands on T1-T5 and patch laterally on T6; bands narrower on T1-T2 than on T3-T5. Clypeus broadly smoothly convex, highest basally and centrally, gradually tapering to sides and apex, apex with 6-8 denticles between which arise tufts of light brown hair; mandible with 3 teeth equidistant (as in Fig. 20C); maxillary palpus 4-segmented, small fourth segment not clearly separated from third (Fig. 2C). S6 with thin brown median apical projection (Figs. 12F,14C,16C,18F); S8 bilobed apically (Figs. 12E,14F,16D,18E); gonoforceps with cleft separating small lateral tooth (Figs. 12A,14A,16A,18A).

FEMALE: Agrees with description of male except for sex limited characters and pale hair bands only on T1-T4.

Trachusa manni Crawford

Figs. 1B,1I,11C-11F,12A-12F, Map 3

Trachusa manni Crawford, 1917, p. 167.

MALE: Length 15 mm; forewing length 10 mm (8 mm from tegula to tip cell M). Integument black except tip of mandible and inner surfaces of legs dark red brown. Pubescence of thoracic dorsum and vertex straw yellow; S3-S5 apical hair bands very dense and hairs plumose; hair of metasomal terga other than white marginal bands erect, long on T1, short on T2-T6, appressed on T7 basolaterally. Punctures more than 1 diameter apart on basal half of clypeus,

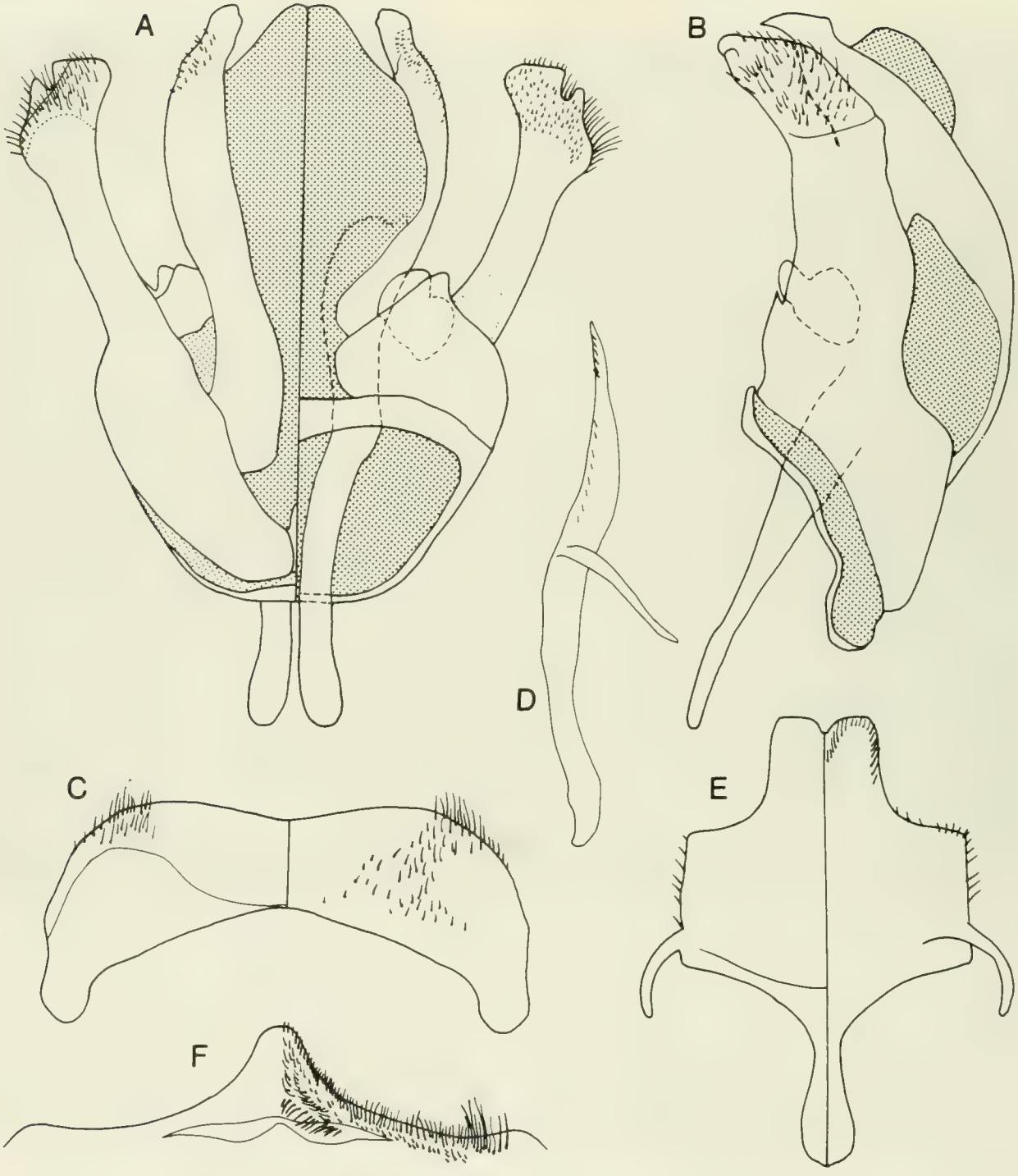


Fig. 12. Male terminalia of *Trachusa manni*. In divided views (A,C,E) right side is ventral and left is dorsal. All figures drawn to same scale. **A,B,** genital capsule, dorsoventral and side views; **C,** S7, dorsoventral view; **D,E,** S8, side and dorsoventral views; **F,** S6, ventral view of apical margin.

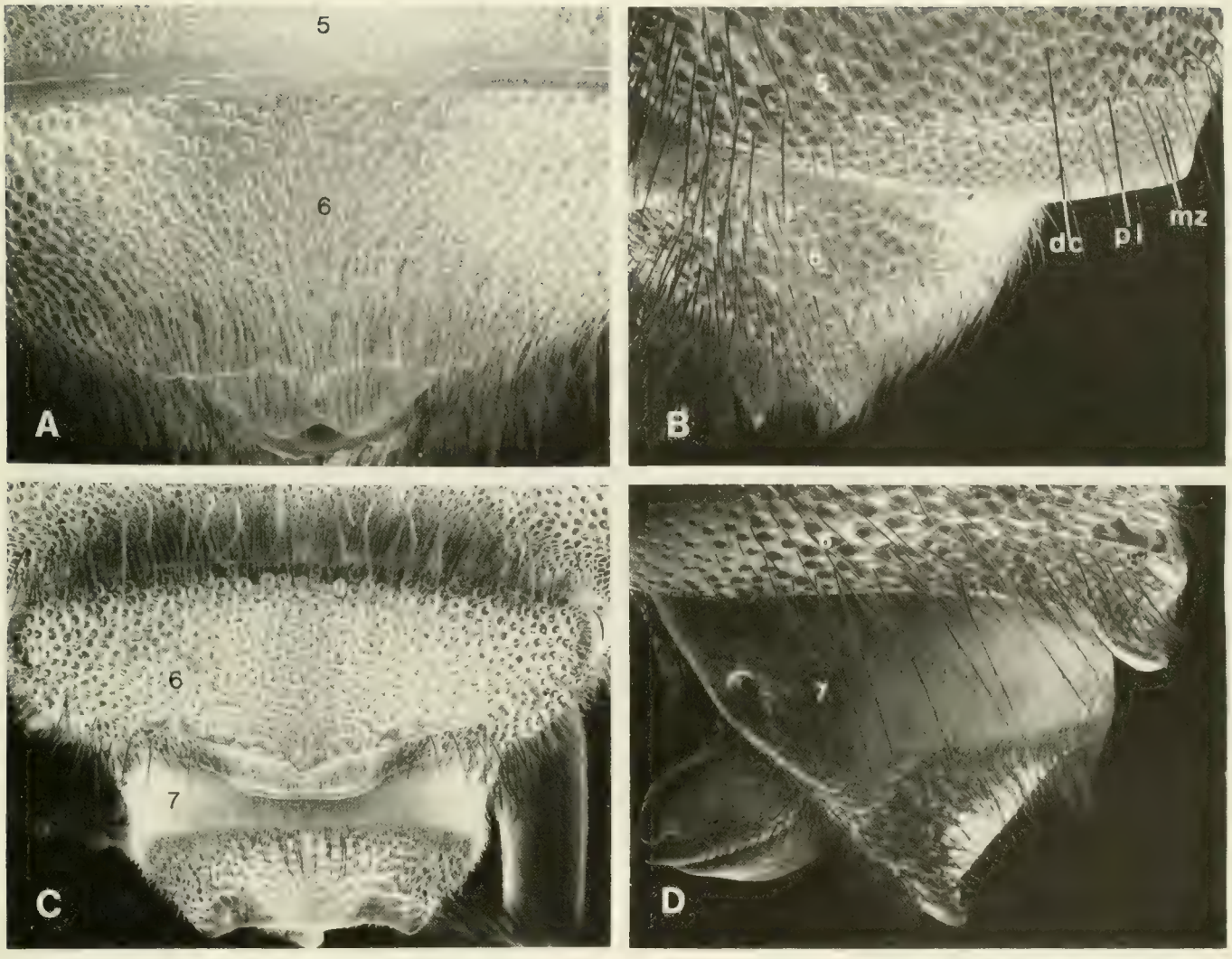


Fig. 13. *Trachusa alamosana* metasomal apices. dc = dorsal convexity; mz = marginal zone; pl = premarginal line. **A,B,** female T6, dorsal and side views; **C,D,** male T7, dorsal and side views. In B and D dorsal surfaces are to the right.

finest on upper face and gena, contiguous on thoracic dorsum, separated by less than 1 diameter elsewhere. Ocellocular distance equal to (posterior) interocellar distance; T6 with truncate apex about half as wide as T7 and subapical transverse ridge obscured medially (Figs. 1B,11E); T7 with two large triangular subapical lateral protuberances (Fig. 11E); S8 shallowly emarginate apically to more or less right angled shoulders and with rectangular mid section (Fig. 12E); penis valves narrowed subapically, expanded and pick-like apically (Figs. 12A,12B).

FEMALE: Length 14 mm; forewing length 11 mm [8.5 from tegula to tip cell M]. Agrees with description of male except sex limited characters; pubescence of clypeus short centrally, coppery, some hairs bent at apices, some long plumose hairs apically on clypeus. Punctures less than 1 diameter apart on basal half of clypeus. T6 moderately densely covered with short appressed silvery white hair; scopa coppery. T6 with median basal process and subapical pair of lateral low ridges separated medially; median apical flange weakly bilobed (Figs. 1I,11C); T5-T3 with dorsal convexities and marginal zones like *T. alamosana* (Figs. 13B, 14H).

Distribution: *Trachusa manni* is known from southern Arizona (Map 3). The type and paratype males are from Ramsey Canyon, Huachuca Mountains, Cochise County, Arizona. We have examined an additional 8 males and 4 females from the following localities: **Arizona**: *Cochise Co.*: 1M, Palmerlee, [19 km W. Hereford, Reef Mine on Miller Creek, Huachuca Mts., no date, no collector]; 1M, Huachuca Mts., Oslar (LACM); 1F, Carr Canyon, 5400' (1646m), 21-23 August 1972, and 1F, 6500' (1981m), 24 August 1972, R. R. Snelling (LACM); 1M, Carr Canyon, 2 mi. (3.2km) W., 10 September 1985, R. W. Thorp (RMBM); 1M, Miller Canyon, 11 September 1979, Knowlton, Hanson (USU). *Pima Co.*: 1M,1F, Madera Canyon, 24 August 1977, *Trichostema arizonicum*, R. W. Brooks (SEM); 1M, Madera Canyon, Boggs Springs, 30-31 July 1973, J. Powell, R. Coville, S. Szerlip, at black light (UCB); 1M, Tucson, 4 mi. (6.4km) W., 2 September 1963, V. L. Vesterby (RMBM). *Santa Cruz Co.*: 1F, 15 mi. (24km) E. Nogales, 22 September 1963, V. L. Vesterby (RMBM).

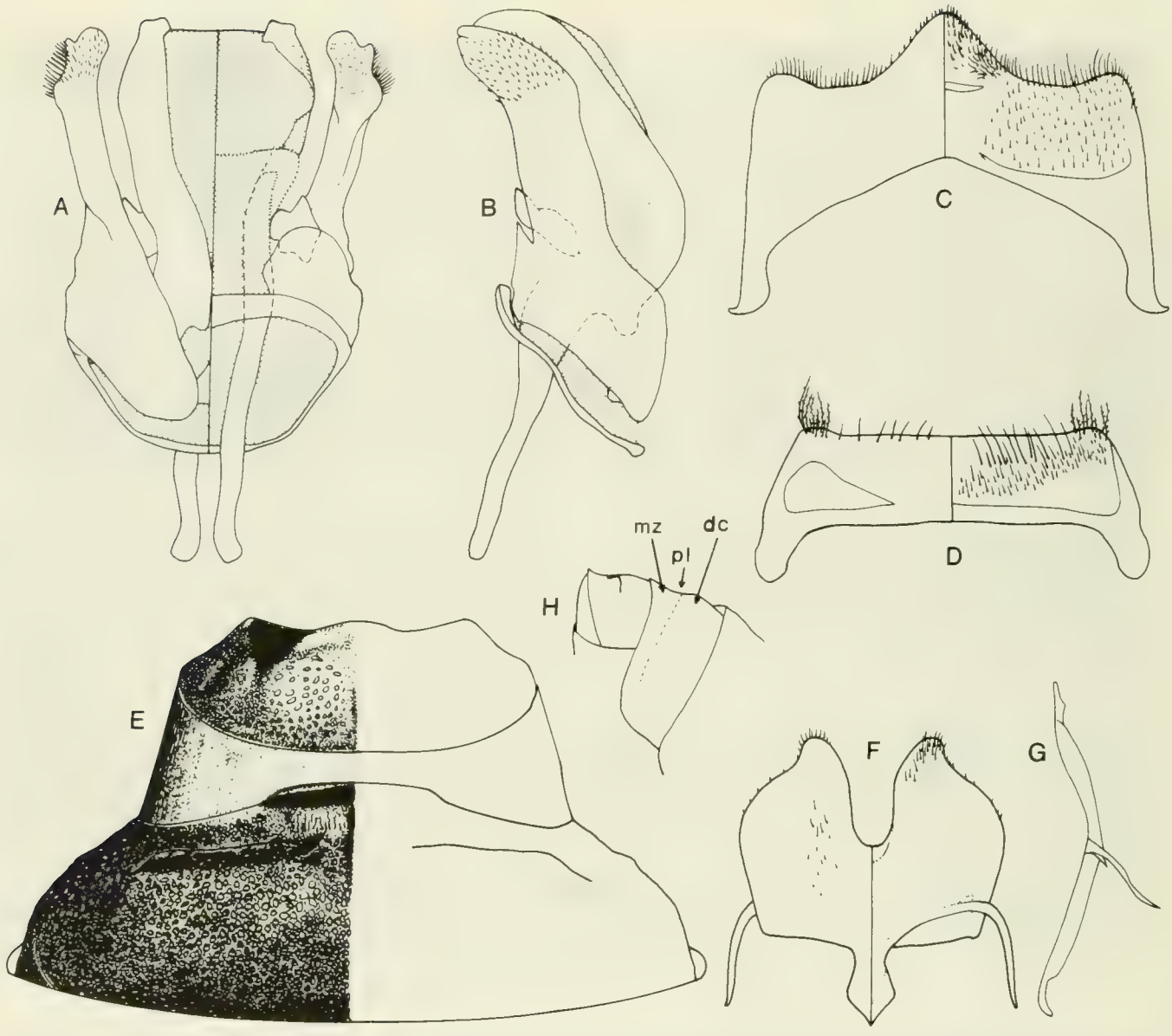


Fig. 14. Male terminalia of *Trachusa alamosana*. In divided views (A,C,D,F) right side is ventral and left is dorsal. All figures drawn to same scale. dc = dorsal convexity; mz = marginal zone; pl = premarginal line. **A,B,** genital capsule, dorsoventral and side views; **C,** S6, dorsoventral view; **D,** S7, dorsoventral view; **E,** T6 and T7, dorsal view; **F,G,** S8, dorsoventral and side views; **H,** apex of female metasoma, side view.

Flight records: Males have been taken from 30 July to 11 September, females from 21 August to 22 September.

Trachusa alamosana new species

Figs. 1A,1H,10B,10D,13A-13D,14A-14H, Map 3

MALE: Length 13 mm; forewing length 9 mm (7.5 mm from tegula to tip of cell M). Integument black except antenna below, inner surfaces of legs and T7 medioapically mahogany. Pubescence above antennae, vertex, thoracic dorsum and apical band of T1 dark yellow; apical bands of T2-T3 cream, hairs dense and somewhat appressed on scutum; hair of T1-T5 other than pale marginal bands erect, moderately long; of T6-T7 short and appressed. Ocellar diameter greater than distance between ocelli. Punctation like *T. manni*. T6 with subapical ridge bending apicad medially as shallow V not reaching apex, apical truncate shelf about half width of T7 (Figs. 1A,13C); T7 with two widely separated subapical projections and bare shiny central area (Fig. 13C); S8 deeply emarginate, cleft about half depth of disc, shoulders sloped and rounded (Fig. 13F); penis valve narrowed subapically, expanded laterally to point (Figs. 13A,13B).

FEMALE: Length 13 mm; forewing length 9.5 mm (7.5 mm from tegula to tip cell M). Agrees with description of male except for sex limited characters; pubescence of clypeus short, sparse, coppery with some hairs hooked at tips and some long plumose hairs

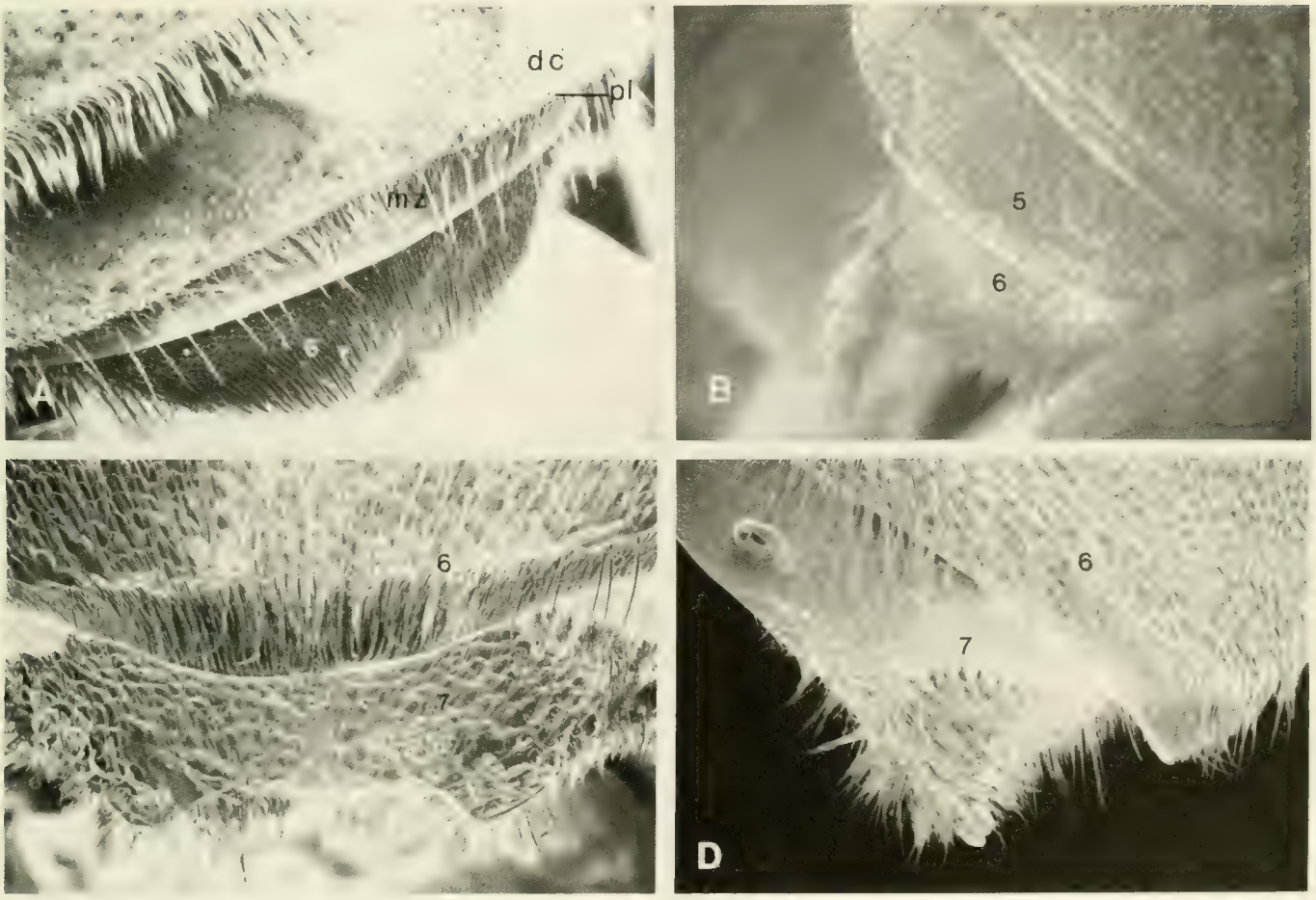


Fig. 15. *Trachusa notophila* metasomal apices. dc = dorsal convexity; mz = marginal zone; pl = premarginal line. **A,B,** female T6, oblique and lateral views; **C,D,** male T7, dorsal and lateral views. In B dorsal surface is to the left; in D to right.

apically (Figs. 10B,10D). Punctation like *T. manni*. Median apical half of T6 densely covered with fine appressed silvery white hair but integument still visible (Fig. 13A); scopa straw-yellow; clypeus with indication of median longitudinal ridge; T6 swollen mediobasally with pair of subapical lateral low ridges separated medially by flat to convex area; median apical flange barely bilobed; T3-T5 with dorsal convexities and marginal zones at wide obtuse angles to each other, almost flat such that premarginal line is weakly defined (Figs. 13B,14H).

Type material: The type male and 14 male and 11 female paratypes come from a small region near the juncture of the states of Sonora, Sinaloa and Chihuahua, México (Map 3). The holotype male, allotype and 2 paratypes (1F,1M) were collected at Alamos, Sonora, 7 September 1977, on *Antigonon leptopus* [Polygonaceae], R. W. Brooks (SEM). The following paratypes were also collected at **Sonora**: Alamos: 1M, 2 October 1933, G. E. & R.M. Bohart (USNM); 2M, 5 September 1970, R. M. Bohart (RMBM); 4M,1F, 7 September 1970, G. E. & R. M. Bohart (USU); 1M, 6 September 1970, W. J. Hanson & T. L. Whitworth (USU); 1M, 29 August 1971, J. L. Petty (USU); 1M,1F, 6 September 1971, J. L. Petty (USU); 3M,1F, W. J. Hanson (USU); 1M, 27 August 1976, Hanson & Schwartz (USU);. Additional paratypes include: **Chihuahua**: 1F, Temoris, 13 September 1969, T. A. Sears, R. C. Gardner, C. S. Glaser (RMBM). **Sinaloa**: 1F, Choix, 4 mi. (6.4km) NW, Arroyo del Saucilio, 2 September 1968, T. A. Sears, R. C. Gardner, C. S. Glaser (RMBM) and 2F, Choix, 5.5 mi. (8.8km) NW., 5 September 1968, T. A. Sears, R. C. Gardner, C. S. Glaser (RMBM).

Trachusa notophila new species

Figs. 1C,15A-15D,16A-16G, Map 3

MALE: Length 14 mm; forewing length 11 mm (9 from tegula to tip of cell M). Integument as in *T. alamosana*. Pubescence of thoracic dorsum, vertex, inner surfaces of basitarsi and above antennae light foxy red; of rest of body light yellow except T6-T7 coppery; hair of metasomal terga other than pale marginal bands erect, long on T1, short on T2-T5, short and appressed on T6-T7. Ocellocular distance greater than (posterior) interocellar distance. Punctation as in *T. manni*. Clypeus broadly truncate apically and with shallow dimples basolaterally; T6 with pair of lateral subapical low ridges, apex rounded and produced (Fig. 1C); T7 coarsely punctate centrally and with two widely separated subapical projections (Figs. 15C,15D); S8 emarginate with cleft about sixth length of disc, shoulders sloped (Fig. 16D); penis valves narrowed subapically with apex thickened and acute, apodemes strongly curved ventrally (Figs. 16A,16B).

FEMALE: Length 14 mm: forewing length 10.0 mm [8.4 mm from tegula to tip of cell M]. Agrees with description of male except sex limited characters; pubescence of clypeus gently curving,

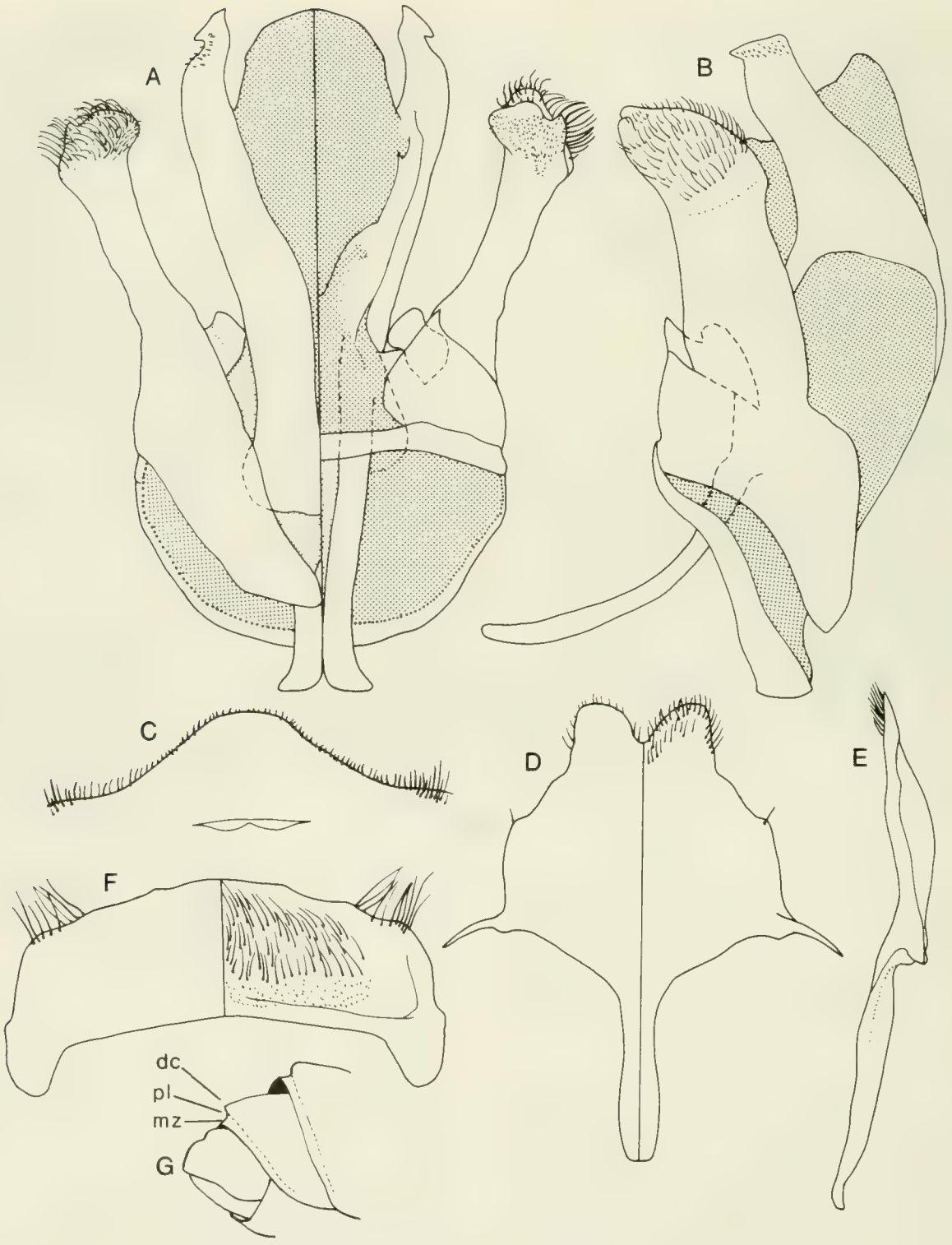


Fig. 16. Male terminalia of *Trachusa notophila*. In divided views (A,D,F) right side is ventral and left is dorsal. All figures drawn to same scale. dc = dorsal convexity; mz = marginal zone; pl = premarginal line. **A,B,** genital capsule, dorsoventral and side views; **C,** S6, ventral view of apical margin; **D,E,** S8, dorsoventral and side views; **F,** S7, dorsoventral view; **G,** apex of female metasoma, side view.

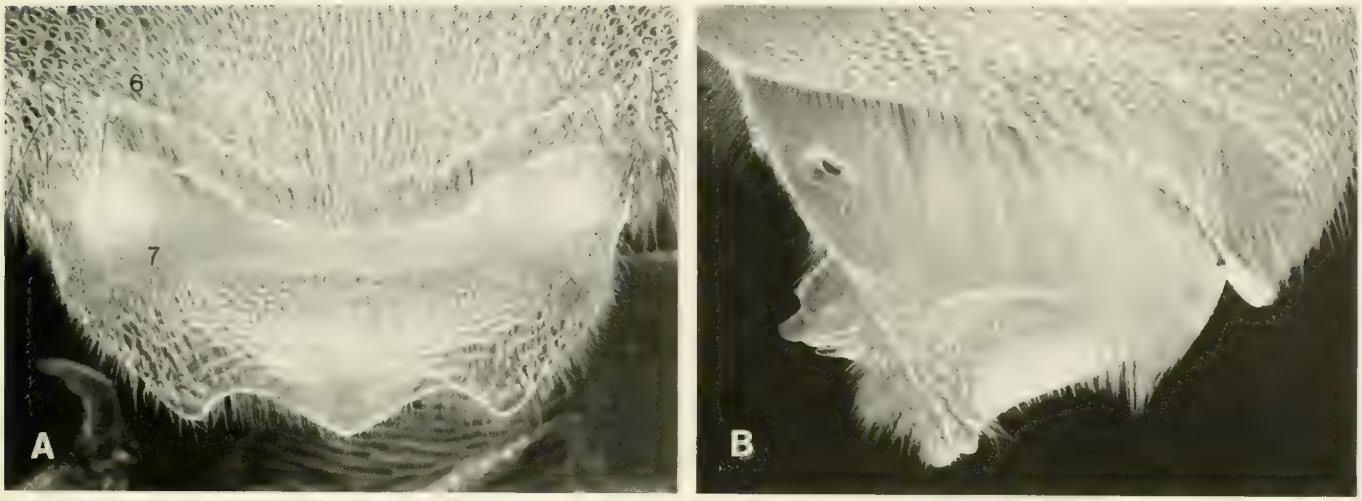


Fig. 17. Metasomal T6 and T7 of *Trachusa pueblana*, male. **A,** dorsal view; **B,** lateral view, dorsal surface to right.

short, thin, coppery and hairs increasing in length gradually toward apical margin; on outer surfaces of legs light foxy red; scopa light foxy red. Punctation as in *T. manni*. Clypeus with indication of median longitudinal ridge; T6 swollen with pair of low subapical lateral ridges separated medially by broad concavity (Fig. 15A), apical flange weakly bilobed medially; T3-T5 with dorsal convexities at right angles to marginal zones such that premarginal line is well defined (Figs. 15A,16G).

Type material: The holotype male and allotype are from 36.7 km NE. Arteaga on Hwy. 37, Michoacán, México, 16 July 1989 on *Vitex pyramidata* [Verbenaceae], R. W. Brooks #052 (SEM). Paratypes include: **Jalisco**: 1M, 3 mi. (4.8km) NW. Tequila, 4000 ft. (1219m), 19 July 1953, *Vitex pyramidata*, Univ. Kansas Mexican Expedition (SEM); 1F, Estación de Biología, Chamela, 5 August 1986, M. Sánchez (EBC). **Oaxaca**: 1M, Oaxaca, bearing no other label information (LACM).

Trachusa pueblana new species

Figs. 1D,17A,17B,18A-18F, Map 3

MALE: Length 13 mm; forewing length 9.5 mm (8 from tegula to tip cell M). Integument as in *T. alamosana*. Pubescence on vertex of head, thoracic dorsum, metasomal terga other than white marginal bands straw yellow; S2-S5 with apical hair bands sparse; hair long on T1, short and suberect on T2-T5, short and appressed on T6-T7. Ocellocular distance subequal to (posterior) interocellar distance; T6 with apical flange and subapical lateral ridges (Fig. 17A); T7 trilobed subapically, lobes somewhat pointed (Figs. 1D,17A); S8 strongly emarginate apically, cleft about third length of disc, sloping to angled shoulders (Fig. 18E); penis valves narrowed subapically curving to apical oblique truncation (Figs. 18A,18B).

FEMALE: Unknown.

Type material: The holotype is from Cuernavaca, Morelos, México, 5 November 1922, E. G. Smyth (SEM). The paratypes are from Morelos and Puebla, México (Map 3). **Morelos**: 2M, Cuernavaca, 8 November, 6 December 1987, F. D. Parker (USU). **Puebla**: 1M, El Tepenene, 10 mi. (16.1 km) SE. Izúcar de Matamoros, 4500' (1372m), 8 October 1975, J. Powell, J. A. Chemsak, T. Eichlin, T. Friedlander (UCB); 1M, Rt. 190, 5 mi. (8km) N. Chila, 14 October 1975, J. L. Neff (CTMI); 1M, 1 km NE. Tepexco, 1120m, 31 October 1991, T. Griswold (USU); 1M, 1 km SW. Petlalcingo, 1280m, 1 November 1991, T. Griswold (USU); 1M, 8 km NW. Acatlán, 1170m, 1 November 1991, T. Griswold (USU).

Interdisciplinaris Group

The presence of all black faces in males, female characteristics such as the clypeal hair plumosity and its length mostly longer than the length of flagellomere 1, apical margin of T5 with wide median process (Figs. 1J,1K), and T6 with strong subapical longitudinal ridge (Figs. 19A,19E) are diagnostic for this group. The two species, *T. interdisciplinaris* and *T. nigrifascies*, are further characterized in the males by having a well developed rounded apical median process on T7 without a lateral protuberance (Figs. 1E,1F,19C).

MALE: Face black without pale markings; wings only lightly stained brown. Pubescence of clypeus long and plumose, hair largely hiding face; T1-T5 with dense apical bands; T6 with lateral patch; T7, except median apical area, nearly bare; apical hair bands narrower on T1-T2 than on T3-T5. Clypeus swollen basally, flattened apically with 5-6 denticles between which arise tufts of light brown hair; mandible with three equidistant teeth (Fig. 20C); maxillary palpus 4-segmented, small fourth segment not clearly separated from third; scutellum weakly depressed along midline, thus biconvex; second recurrent vein distal to second transverse cubital by about two vein widths; T1-T6 with margins strongly depressed, hidden by hairs except for T6; penis valves projecting beyond gonoforceps.

FEMALE: Agrees with male except sex limited characters; hair of face less dense; apical hair bands on T1-T4; ocellocular distance equal to (posterior) interocellar distance; ocellar diameter slightly less than distance between ocelli; denticles of clypeal margin small; teeth of mandible broader (Fig. 20D); apical margin of T5 with median third slightly truncately produced, the produced portion hairless; T6 with longitudinal median ridge highest basally, apical flange produced as narrow, rounded or subtruncate median projection but elsewhere absent so that except medially there is no depressed margin or preapical concavity (Figs. 1J,1K,19A,19E).

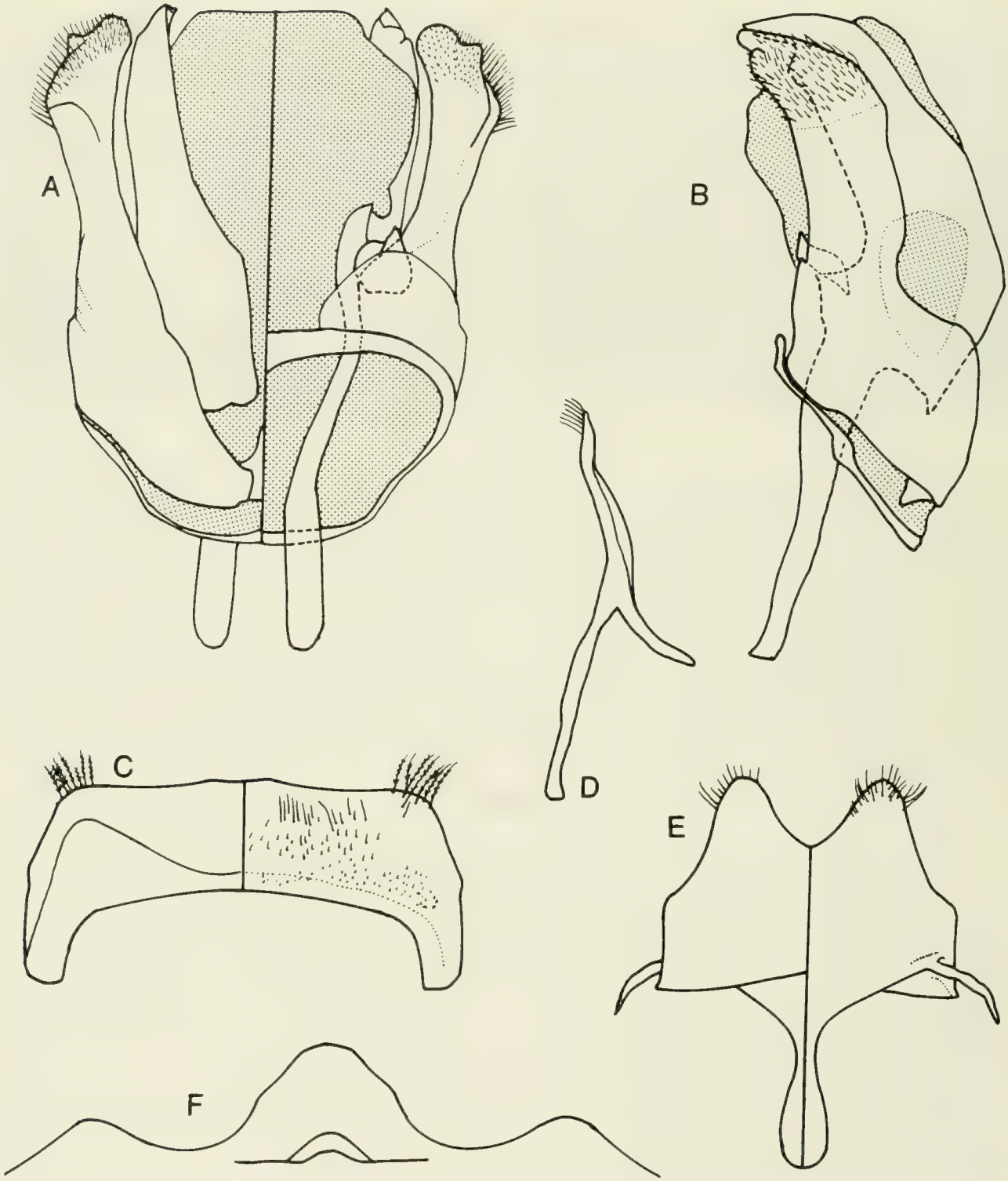


Fig. 18. Male terminalia of *Trachusa pueblana*. In divided views (A,C,E) right side is ventral and left is dorsal. All figures drawn to same scale. **A,B,** genital capsule, dorsoventral and side views; **C,** S7, dorsoventral view; **D,E,** S8, side and dorsoventral views; **F,** S6, ventral view of apical margin.

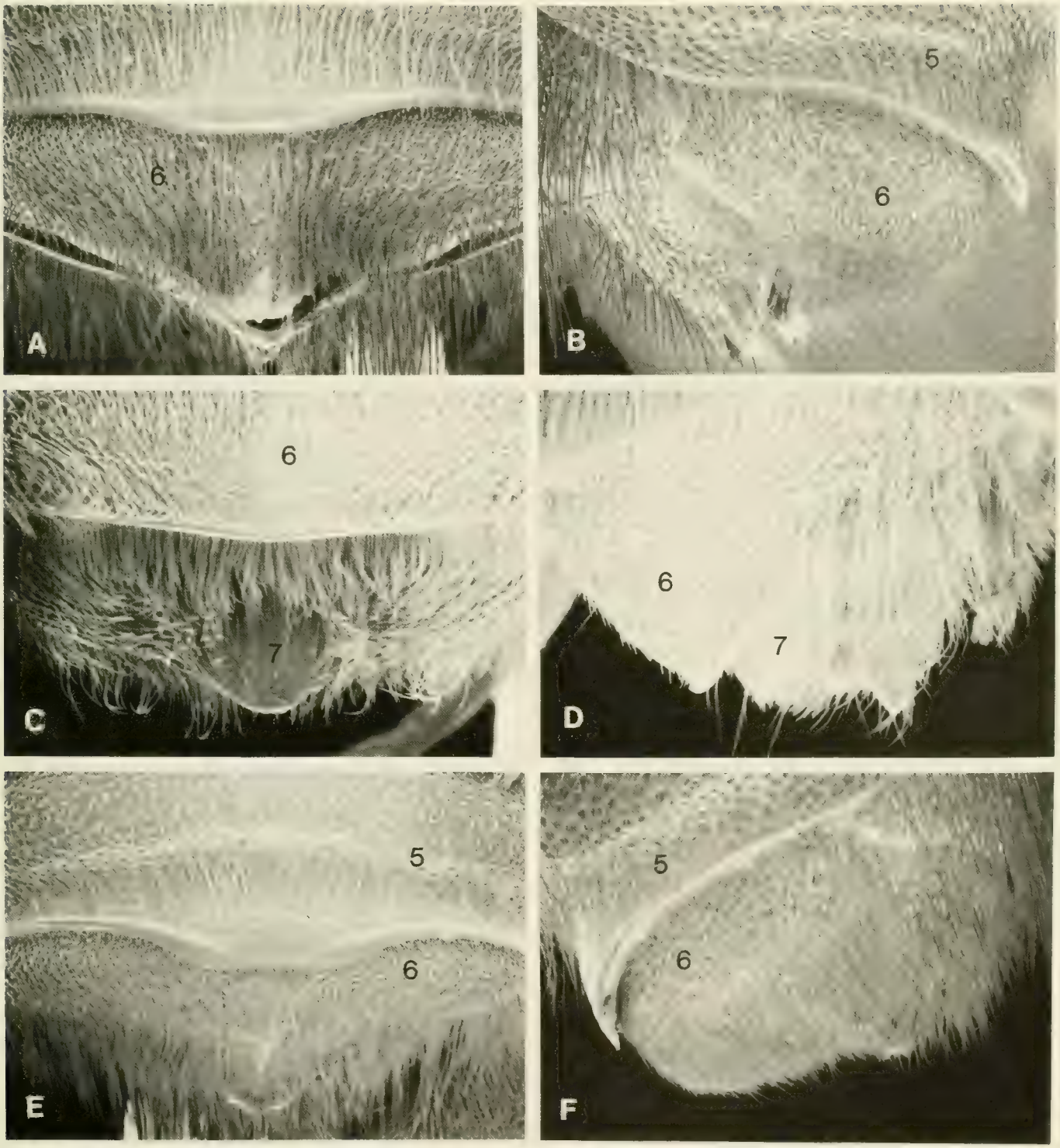


Fig. 19. Metasomal apices of Interdisciplinaris Group. A-D, *Trachusa interdisciplinaris*. **A,B,** female T5,T6, dorsal and side views; **C,D,** male T6, T7, dorsal and side views; **E,F,** *T. nigrifascies*, female T5, T6, dorsal and side views. In B, dorsal surface is to the right; in D and F, to left.

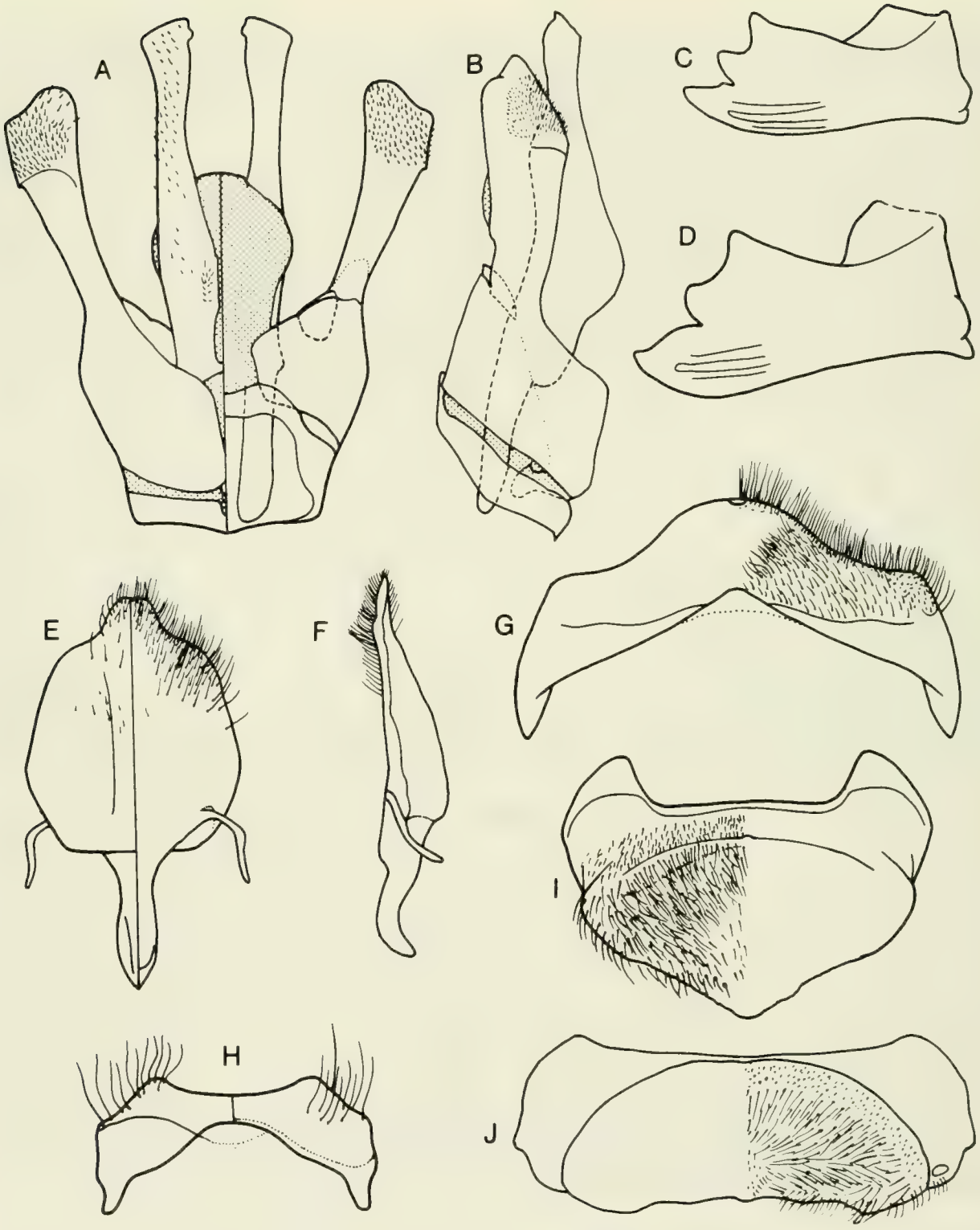


Fig. 20. Male terminalia and mandibles of both sexes of *Trachusa interdisciplinaris*. In divided views (A,E,H) right side is ventral and left is dorsal. All figures drawn to same scale. **A,B,** genital capsule, dorsoventral and side views; **C,D,** male and female mandibles, respectively, outer views; **E,F,** S8, dorsoventral and side views; **G,** S6, ventral view; **H,** S7, dorsoventral view; **I,J,** T7, dorsal and apical views.

Map 3. The distribution of species in the Manni Group.

***Trachusa interdisciplinaris* (Peters)**
Figs. 1E,1J,19A-19D,20A-20J, Map 4

Ulanthidium (*Olmecanthidium*) *interdisciplinaris* Peters, 1972, p. 377.

This species, described from the state of Puebla, has also been found in New Mexico. The description is based on New Mexican and type material.

The body is robust, black, with abundant, rather long white hair and white tergal hair bands on the metasoma, suggesting *Diadasia* or *Anthophora*.

MALE: Length 12 mm; forewing length 9 mm (7.5 mm from tegula to tip of cell M). Black except midapical part of T7 red-brown. Pubescence of metasomal terga other than white marginal bands erect and dusky. Small, triangular, smooth spot medially at extreme base of clypeus; extreme lower margin of supraclypeal area smooth and shining. T7 with weak median longitudinal carina and rounded, flat, weak, translucent, median apical projection and tapering broadly to weak lateral shoulders, ventral margin straight (Figs. 19C,20I,20J); S6 with apical thickening bilobed; S8 with small apical protuberance and sloping rounded shoulders (Fig. 20E); penis valves with apex, bluntly pointed, broader than shaft, but no distinct subapical narrowing (Figs. 20A,20B).

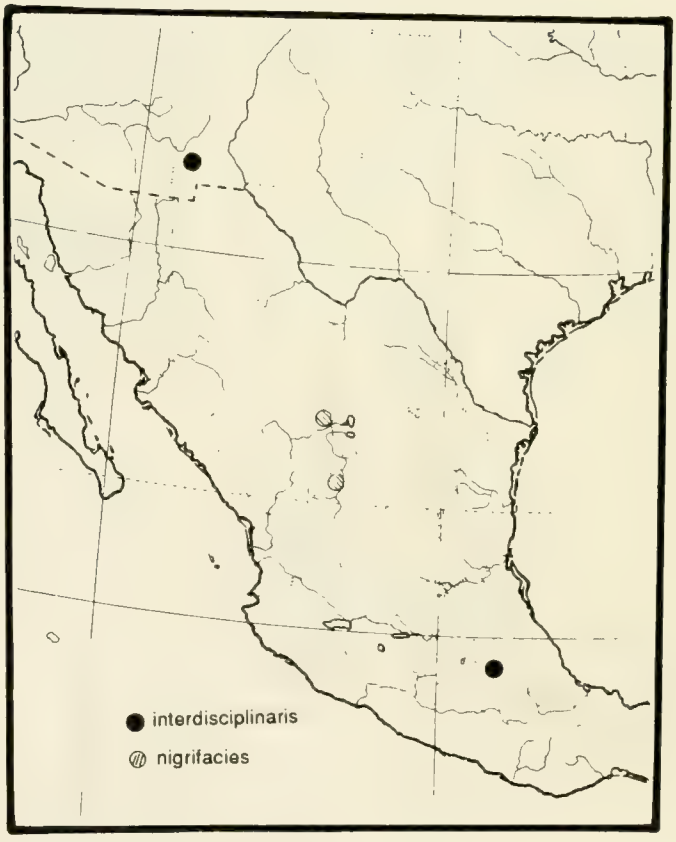
FEMALE: Length 11 mm; forewing length 8.5 mm [7 mm from tegula to tip of cell M]. Agrees with description of male except sex limited characters; no red-brown area at metasomal apex; margin of T5 brown medially. Pubescence of median apical half of T6 densely covered with silvery white hair; scopa straw yellow. Ocellocular distance greater than (posterior) interocellar distance. T6 with a median basal swelling and longitudinal medial carina hidden by hair (Fig. 19A).

The type material from the Pyramid of Totimehuacán, Puebla, México, Oct. 31, 1966, is in the Forschungsinstitut Senckenberg, Frankfurt. The holotype male and three male paratypes were kindly sent for comparison with our New Mexico material. The New Mexico material consisted of 4M,1F, 4 mi. (6.4 km) N. Silver City, Grant Co., September 15, 1975, T. Snyder (SEM) and 30M,14F, 16 September, 1989, R. W. Thorp, on *Dalea albiflora* [Leguminosae], 1M, on *Hymenothrix wrightii* [Compositae], 2M,1F, no floral hosts (all at RMBM, except 1M,1F at SEM) (Map 4). It is possible that the late season of flight explains the failure of North American bee collectors to discover this species before 1975.

The type material from México agrees with specimens from New Mexico, USA, except for the more yellowish or reddish color of the dorsal hairs, particularly of the middorsal parts of the tergal hair bands, and especially those of T3 and T4. More yellowish or reddish pubescence is characteristic of central Mexican populations of various other bee species with largely whitish hairs in the southwestern United States.

***Trachusa nigrifascies* new species**
Figs. 1F,1K,19E,19F,21A-21G, Map 4

MALE: Length 13 mm; forewing length 9 mm (7.5 mm from tegula to tip of cell M). Integument black except inner surfaces of legs and metasomal sterna red brown. Pubescence white except on vertex of head, thoracic dorsum and T1-T5 straw yellow. Hair of metasomal terga other than marginal bands erect and sparse. T6 with broad median apical flange like *T. interdisciplinaris* (Fig. 1F); T7 with broad median apical flange more prominent (Figs. 1F,21D) and end on view more ventrally emarginate (Fig. 21C) than *T. interdisciplinaris*; S6 with subapical thickening bilobed with



Map 4. The distribution of species in the Interdisciplinaris Group.

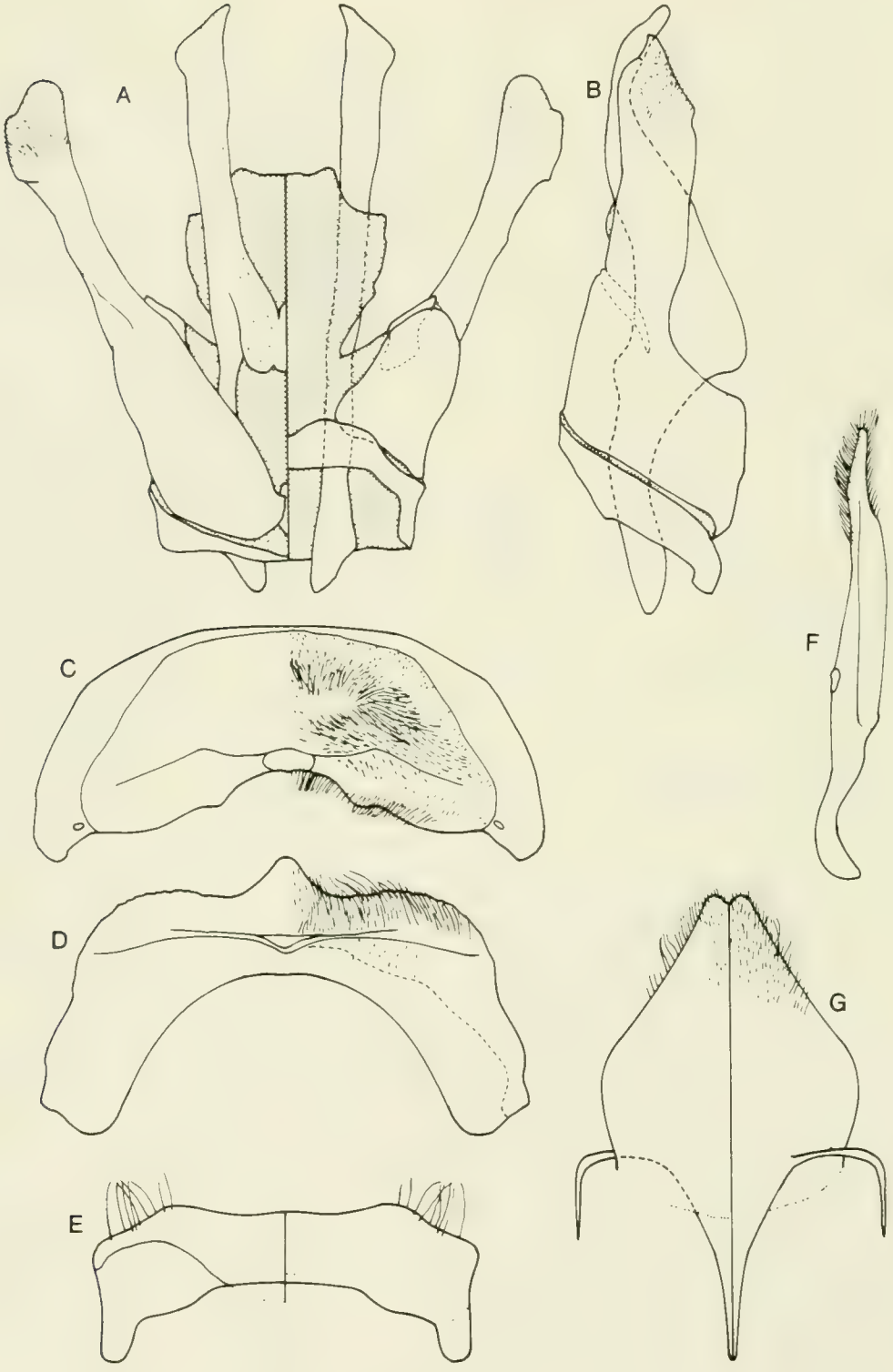


Fig. 21. Male terminalia of *Trachusa nigrifascies*. In divided views (A,E,G) right side is ventral and left is dorsal. All figures drawn to same scale. **A,B,** genital capsule, dorsoventral and side views; **C,D,** T7, apical and dorsal views; **E,** S7, dorsoventral view; **F,G,** S8, side and dorsoventral views.

lobes acute; S8 with shallowly emarginate apex evenly tapered to low rounded shoulders (Fig. 21G); penis valves with apex broader than shaft, but no distinct subapical narrowing, apex pointed mesally (Figs. 21A,21B).

FEMALE: Length 12 mm; forewing length 8.5 mm (7 from tegula to tip M cell). Agrees with description of male except sex limited characters; margin of T4 with apicomedian projection (Fig. 1K); T5 with truncate brown flange medially (Fig. 19E). Pubescence white except scutal hairs paler and shorter; hairs of face less dense; T6 densely covered with appressed white hair; scopa coppery. T4 with apex produced as small V medially; T6 as in *T. interdisciplinaris* but with more sinuate profile (Figs. 19E,19F).

The type material comes from the northcentral Mexican states of Durango and Zacatecas (Map 4). The holotype male is from Coyotes, Durango, 8300 ft. (2530m), 8 August 1947, C. Michener (D. Rockefeller Expedition), American Museum of Natural History, New York. The allotype female is from Río Grande, Zacatecas, 4 October 1966, on *Helianthella?*, G. E. & A. S. Bohart (USU).

LITERATURE CITED

Brooks, R. W. and T. L. Griswold. 1988. A key to the species of *Trachusa* subgenus *Heteranthidium* with descriptions of new species from Mexico (Hymenoptera: Megachilidae; Anthidiini). Journal of the Kansas Entomological Society 61:332-346.

Cockerell, T. D. A. 1904. The bees of Southern California. VI. Bulletin of the Southern California Academy of Sciences 3:159-162.

Crawford, J. C. 1917. New Hymenoptera. Proceedings of the Entomological Society of Washington 19:165-172.

Dobson, H. E. M. 1993. Bee fauna associated with shrubs in two California chaparral communities. Pan-Pacific Entomologist 69:77-94.

Grigarick, A. A. and L. A. Stange. 1968. The pollen-collecting bees of the Anthidiini of California (Hymenoptera: Megachildae). Bulletin of the California Insect Survey 9:1-113.

Griswold, T. L. and C. D. Michener. 1988. Taxonomic observations on Anthidiini of the Western Hemisphere (Hymenoptera: Megachilidae). Journal of the Kansas Entomological Society 61:22-45.

Michener, C. D. 1941. A synopsis of the genus *Trachusa* with notes on the nesting habits of *T. perdita* (Hymenoptera, Megachilidae). Pan-Pacific Entomologist 17:119-125.

Michener, C. D. 1948. The generic classification of the anthidiine bees (Hymenopera: Megachilidae). American Museum Novitates no. 138:1-29.

Michener, C. D. and E. Ordway. 1964. Some anthidiine bees from Mexico (Hymenoptera: Megachilidae). Journal of the New York Entomological Society 72:70-78.

Pasteels, J. J. 1969. La systematique generique et subgenerique des Anthidiinae (Hymenoptera, Apoidea, Megachilidae) de l'Ancien Monde. Memoires de la Société Royale d'Entomologie de Belgique 31:1-148.

Pasteels, J. J. 1977. Une revue comparative de l'éthologie des Anthidiinae nidificateurs de l'Ancien Monde [Hymenoptera, Megachilidae]. Annales de la Société Entomologique de France (N.S.) 13:651-667.

Peters, D. S. 1972. Drei neue Arten der Megachilidae aus Mexico (Insecta: Hymenoptera: Apoidea). Senckenbergiana Biologica 53:373-382.

Popov, V. B. 1964. On the genera *Trachusa* Panzer and *Trachusomimus*, gen. n. (Hymenoptera, Megachilidae). Revue d'Entomologie de l'URSS 43:405-417 [in Russian].

Thorp, R. W. 1963. A new species of the genus *Trachusa* from California with a key to the known species (Hymenoptera: Megachilidae). Pan-Pacific Entomologist 39:56-58.

Thorp, R. W. 1966. Synopsis of the genus *Heterostelis* Timberlake (Hymenoptera: Megachilidae). Journal of the Kansas Entomological Society 39:131-146.

ANNOUNCEMENT

The *University of Kansas Science Bulletin* (continuation of the *Kansas University Quarterly*) is an outlet for scholarly scientific investigations carried out at the University of Kansas or by University faculty and students. Since its inception, volumes of the *Bulletin* have been variously issued as single bound volumes, as two or three multi-paper parts or as series of individual papers. Issuance is at irregular intervals, with each volume prior to volume 50 approximately 1000 pages in length. Effective with volume 50, page size has been enlarged, reducing the length of each volume to about 750 pages.

The supply of all volumes of the *Kansas University Quarterly* is now exhausted. However, most volumes of the *University of Kansas Science Bulletin* are still available and are offered, in exchange for similar publications, to learned societies, colleges and universities and other institutions, or may be purchased at $30.00 per volume. Where some of these volumes were issued in parts, individual parts are priced at the rate of 3 cents per page. Current policy, initiated with volume 46, is to issue individual papers as published. Such separata may be purchased individually at the rate of 7 cents per page, with a minimum charge of $1.50 per separate. Subscriptions for forthcoming volumes may be entered at the rate of $30.00 per volume. All communications regarding exchanges, sales and subscriptions should be addressed to the EXCHANGE LIBRARIAN, UNIVERSITY OF KANSAS LIBRARIES, LAWRENCE, KANSAS 66045.

Reprints of individual papers for personal use by investigators are available for most recent and many older issues of the *Bulletin*. Such requests should be directed to the author.

The International Standard Serial Number of this publication is US ISSN 0022-8850.

Editor
Charles D. Michener

Editorial Board
Meredith Lane, *Chairman*
James S. Ashe
George W. Byers
Christopher Haufler
Norman A. Slade

THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. 55, No. 9, pp. 299-327 October 20, 1994

NOV 28 1994

HARVARD
UNIVERSITY

The Classification of Old World Anthidiini (Hymenoptera, Megachilidae)

CHARLES D. MICHENER[1] AND TERRY L. GRISWOLD[2]

TABLE OF CONTENTS

Abstract 299
Introduction 300
Acknowledgments 300
List of Genus-Group Names 300
Key to the Genera of Anthidiini of the Eastern Hemisphere 302
Supplementary Key to Males of Anthidiine Genera of the Eastern Hemisphere 304
Comments, Descriptions, and Keys to Subgenera 305
(See page numbers for genera in List of Genus-Group Names)
Literature Cited 325

ABSTRACT

Genus-group names of Anthidiini of the eastern hemisphere are listed with indications of synonymies and status (i.e., genus or subgenus). Keys to genera and subgenera are provided, together with explanations of classificatory decisions. The following new taxa are described: *Acanthidium* n. g., type species: *Acanthidium batrae* n. sp. from India; *Clistanthidium*, n. subg. of *Eoanthidium*, type species: *Dianthidium turnericum* Mavromoustakis; *Indanthidium* n. g., type species: *Indanthidium crenulaticauda* n. sp. from India; *Larinostelis* n. g., type species: *Larinostelis scapulata* n. sp. from Kenya; *Trachusoides* n. g., type species: *Trachusoides simplex* n. sp. from India; *Trichanthidiodes*, n. subg. of *Pachyanthidium*, type species: *Pachyanthidium semiluteum* Pasteels; *Zosteranthidium*, n. subg. of *Afranthidium*, type species: *Nigranthidium tergofasciatum* Pasteels; and *Pseudoanthidium brachiatum* n. sp. from Tanzania, an unusual species placed in the subgenus *Tuberanthidium*.

[1] SNOW ENTOMOLOGICAL MUSEUM, UNIVERSITY OF KANSAS, LAWRENCE, KANSAS 66045, USA.
[2] BEE BIOLOGY & SYSTEMATICS LABORATORY, UTAH STATE UNIVERSITY, LOGAN, UTAH 84322-5310, USA.

INTRODUCTION

The preparation of an account of bees of the world by one of us (CDM) led to development of the present paper on old world anthidiine bees, to serve as a precursor for the account planned for the future. The anthidiine bees constitute a tribe in the subfamily Megachilinae in the sense of Roig-Alsina and Michener (1993). We now exclude Dioxyini from the Anthidiini. The Anthidiini differs from other tribes (Dioxyini, Megachilini, Osmiini) in the following characters:

Mandible of female much broader than that of male, with three or more teeth, sometimes difficult to interpret if there is a long and partly smooth apical margin as in some neotropical forms. Metanotum without median tubercle. Stigma less than twice as long as broad, inner margin basal to vein r usually little if any longer than width, rarely about 1.5 times width; prestigma commonly short, usually less than twice as long as broad; claws of female cleft or with inner tooth except in *Trachusoides;* outer surface of hind tibia usually with abundant simple bristles; sting of female well developed; body commonly with yellow or white (sometimes red) integumental marks.

We use some terminology that will be explained elsewhere in greater detail. The following brief explanations will suffice for this paper:

omalus—the angle between the anterior surface and the lateral surface of the mesepisternum.

juxtantennal carinae—the pair of more or less longitudinal carinae, each just mesal to an antennal base and frequently overlapping the antennal base. (Terms like interantennal carinae suggest carinae extending between the antennal bases.)

T1, S1, etc.—first metasomal tergum and sternum, etc. Thus, T1 is the second abdominal tergum, the propodeum being first.

This tribe is found in all continents, but only one species is known from Australia. Elsewhere each continent contains many genera and species. There is a tendency for the development of numerous, small, morphologically distinctive taxa so that many genera and subgenera have been recognized. On the other hand Warncke (1980) placed all nonparasitic Anthidiini of the western palearctic region in the genus *Anthidium.* This clearly lumps very dissimilar forms into a paraphyletic group from which parasitic taxa must have evolved.

In the present paper, we ignore taxa of the western hemisphere. Only the following genera occur both in the Americas and in the eastern hemisphere: *Anthidiellum, Anthidium, Trachusa,* and *Stelis.*

We have not included detailed descriptions except for new taxa; this paper requires use of earlier works, especially the major papers by Pasteels (1969a, 1984). We are impressed that, although Pasteels' works showed many signs of haste, he knew a great deal about anthidiine bees. Even though his keys often do not work and his diagrams of structures and his descriptions sometimes conflict or are wrong for certain characters, comprehensive knowledge of anthidiines was advanced by his contributions. Frustrating as his works can be, we must say that a paper such as ours would have been difficult to prepare using the scattered literature available before Pasteels' publications. Nonetheless, we believe that one of the contributions of the present work is better to indicate relationships among taxa by synonymizing some of Pasteels' generic names and reducing many others from generic to subgeneric status.

The new species described herein are all rare, at least in collections; the number of available specimens of each varies from one to four. Therefore we have given rather full descriptions and illustrations, and have included probable generic characters in the species descriptions, so that explicit information will be available on as many characters as possible for the use of those who do not have specimens available.

In the geographical information provided in the keys, Africa means subsaharan Africa and Oriental means the Oriental faunal region, i.e., tropical Asia and nearby islands.

Clearly a numerical phylogenetic study would have been desirable and will be necessary before a more definitive classification is developed, whether or not that classification is based strictly on phylogenetic findings. We hope that the present paper, and the world account alluded to above in which taxa will be briefly characterized, will at least suggest a multitude of characters that might be used in a formal phylogenetic study.

ACKNOWLEDGMENTS

We much appreciate the opportunity to examine type specimens and other material lent us by the following institutions and persons: Zoologisches Museum an der Humboldt-Universität, Berlin (Frank Koch); The Natural History Museum, London (Laraine Ficken); Director, Department of Agriculture, Nicosia, Cyprus; American Museum of Natural History, New York (Jerome G. Rozen, Jr.); California Academy of Sciences, San Francisco (W. V. Pulawski); University of California, Davis (Lynn S. Kimsey); South African Museum, Capetown (V. Whitehead); Zoological Institute, Russian Academy of Sciences, St. Petersburg (Y. A. Pesenko); G. van der Zanden, Eindhoven, Netherlands.

CDM's part in this paper was greatly facilitated by Virginia Ashlock and by National Science Foundation grant DEB-9302186.

LIST OF GENUS-GROUP NAMES

Acanthidium Michener and Griswold, new genus; p. **305**.
Afranthidium Michener; p. **307**.
Afranthidium Michener s. str., 1948: 24.
Branthidium Pasteels, 1969a: 88 = *Honanthidium* Pasteels, 1969a: 88.
Capanthidium Pasteels, 1969a: 85.
Domanthidium Pasteels, 1969a: 95.
Immanthidium Pasteels, 1969a: 89.
Mesanthidiellum Pasteels, 1969a: 83.
Mesanthidium Popov, 1950: 316.

MCZ LIBRARY NOV 28 1995 HARVARD UNIVERSITY

Nigranthidium Pasteels, 1984: 57 = *Melanthidium* Pasteels, 1969a: 90 (preoccupied).
Oranthidium Pasteels, 1969a: 95.
Xenanthidium Pasteels, 1984: 33.
Zosteranthidium Michener and Griswold, new subgenus.
Afrostelis Cockerell, 1931: 340; p. **312**.
Anthidiellum Cockerell; p. **312**.
Ananthidiellum Pasteels, 1969a: 49.
Anthidiellum Cockerell s. str., 1904b: 3 = *Cerianthidium* Friese, 1923: 304.
Chloranthidiellum Mavromoustakis, 1963b: 491 = *Chloranthidium* Pasteels, 1969a: 48 (unjustified emendation).
Clypanthidium Pasteels, 1968: 1060, also described as new in Pasteels, 1969a: 53.
Pycnanthidium Krombein, 1951: 292 = *Pygnanthidium* Mavromoustakis, 1963b: 491 (unjustified emendation) = *Pygnanthidiellum* Mavromoustakis, 1963b: 492.
Ranthidiellum Pasteels, 1969a: 48 = *Rhanthidiellum* Pasteels, 1972: 102 (unjustified emendation).
Anthidioma Pasteels, 1984: 34; p. **313**.
Anthidium Fabricius; p. **313**.
Anthidium Fabricius s. str., 1804: 364 = *Melanoanthidium* Tkalců, 1967: 91 = *Echinanthidium* Pasteels, 1969a: 101 = *Pontanthidium* Pasteels, 1969a: 105 = *Ardenthidium* Pasteels, 1969a: 103 = *Morphanthidium* Pasteels, 1969b: 423. The last is invalid; no indication of a type species, but contains same species as *Ardenthidium*.
Gulanthidium Pasteels 1969a: 101.
Nivanthidium Pasteels, 1969a: 106
Proanthidium Friese, 1898: 101.
Severanthidium Pasteels, 1969a: 106.
Turkanthidium Pasteels, 1969a: 103.
Apianthidium Pasteels, 1969a: 41.
Atropium Pasteels, 1984: 132.
Bathanthidium Mavromoustakis; p. **314**.
Bathanthidium Mavromoustakis s. str., 1953: 837.
Manthidium Pasteels, 1969a: 43.
Stenanthidiellum Pasteels, 1968: 1059 = ? *Lasanthidium* Romankova, 1988: 26.
Benanthis Pasteels, 1969a: 61. Status unknown; p. **314**.
Cyphanthidium Pasteels, 1969a: 57 = *Trianthidiellum* Pasteels, 1969a: 58; p. **314**.
Eoanthidium Popov; p. **314**.
Clistanthidium Michener and Griswold, new subgenus.
Eoanthidium Popov s. str., 1950: 316 = *Eoanthidiellum* Pasteels, 1969a: 51.
Hemidiellum Pasteels, 1972: 112.
Salemanthidium Pasteels, 1969a: 51.
Euaspis Gerstaecker, 1857: 460 = *Dilobopeltis* Fairmaire, 1858: 266 = *Parevaspis* Ritsema, 1874: lxxi; p. **315**.
Gnathanthidium Pasteels, 1969a: 92 (not Urban, 1992); p. **315**.
Icteranthidium Michener, 1948: 25.
Indanthidium Michener and Griswold, new genus; p. **315**.
Larinostelis Michener and Griswold, new genus; p. **317**.
Neanthidium Pasteels, 1969a: 93.
Pachyanthidium Friese; p. **317**.
Ausanthidium Pasteels, 1969a: 60.
Pachyanthidium Friese s. str., 1905: 66, also described as new by Friese, 1908: 158.
Trichanthidiodes Michener and Griswold, new subgenus.
Trichanthidium Cockerell, 1930: 52.
Plesianthidium Cameron; p. **319**.
Carinanthidium Pasteels, 1969a: 42.
Plesianthidium Cameron s. str., 1905: 256.
Spinanthidiellum Pasteels, 1969a: 59.
Spinanthidium Mavromoustakis, 1951: 977.
Pseudoanthidium Friese; p. **319**.
Exanthidium Pasteels, 1969a: 82.
Micranthidium Cockerell, 1930: 45.
Pseudoanthidium Friese s. str., 1898: 101 = *Paranthidiellum* Michener, 1948: 25 = *Paraanthidiellum* Pasteels, 1969a: 80 (unnecessary emendation) = *Carinellum* Pasteels, 1969a: 80.
Royanthidium Pasteels, 1969a: 86 = *Reanthidium* Pasteels, 1969a: 87.
Semicarinella Pasteels, 1984: 32.
Tuberanthidium Pasteels, 1969a: 87.
Rhodanthidium Isensee; p. **321**.
Asianthidium Popov, 1950: 315 = *Trianthidium* Mavromoustakis, 1958: 435 = *Oxyanthidium* Mavromoustakis, 1963a: 653 = *Axillanthidium* Pasteels, 1969a: 39.
Meganthidium Popov, 1950: 315.
Rhodanthidium Isensee s. str., 1927: 374 = *Bellanthidium* Pasteels, 1969a: 38.
Serapista Cockerell, 1904a: 357 = *Serapis* Smith, 1854: 218 (preoccupied).
Stelis Panzer; p. **322**.
Malanthidium Pasteels, 1969a: 26.
Protostelis Friese, 1895: 25 = *Heterostelis* Timberlake, 1941: 125 = *Doxanthidium* Pasteels, 1969a: 28.
Pseudostelis Popov, 1956: 167.
Stelidomorpha Morawitz, 1875: 131.
Stelis Panzer s. str., 1806: 246 = *Gyrodroma* Klug, 1807: 198 = *Gymnus* Spinola, 1808: 9 = *Ceraplastes* Gistel, 1848: x = *Leucostelis* Noskiewicz, 1961: 126. Numerous genus-group names proposed for North American species are also best regarded as synonyms of *Stelis* s. str.
Trachusa Panzer; p. **323**.
Archianthidium Mavromoustakis, 1939: 91.
Congotrachusa Pasteels, 1969a: 24.
Massanthidium Pasteels, 1969a: 24.
Metatrachusa Pasteels, 1969a: 22.
Orthanthidium Mavromoustakis, 1953: 837.
Paraanthidium Friese, 1898: 101 = *Protanthidium* Cockerell and Cockerell, 1901: 49 = *Protoanthidium* Cameron, 1902: 125 = *Philotrachusa* Pasteels, 1969a: 22.
Trachusa Panzer s. str., 1804: expl. pl. 14-15 = *Diphysis* Lepeletier, 1841: 307 = *Megachileoides* Radoszkowski, 1874: 132. See Michener, in press.
Trachusoides Michener and Griswold, new genus; p. **324**.

KEY TO THE GENERA OF ANTHIDIINI OF THE EASTERN HEMISPHERE
(See also Supplementary Key to Males, below.)

1. Mandible of female with 5 to 18, usually sharp teeth separated by acute notches or (in one species of *Pachyanthidium*) minutely denticulate; maxillary palpus short, 2-segmented or in *Indanthidium* apparently 1-segmented (arolia absent; base of propodeal triangle punctate or finely roughened, nearly always hairy; propodeum without basal series of pits and without fovea behind spiracle; juxtantennal carina absent) 2
—Mandible of female with three or four teeth, or if with five to ten, they are rounded and separated by rounded emarginations; maxillary palpus commonly 3- or 4-segmented but sometimes 2-segmented 11
2. T5[3] with posterior premarginal zone depressed (except sometimes medially), more finely punctate than rest of tergum and usually densely so, not over half as wide laterally as medially, this zone ending in very narrow smooth posterior margin, anterior margin of depressed zone often obtusely angulate medially so that whole zone is very broadly triangular 3
—T5 with posterior premarginal zone not depressed or weakly to strongly depressed, this zone if recognizable, punctate like rest of tergum to impunctate, often over half as wide laterally as medially, often ending in broad smooth posterior margin, anterior margin of depressed zone straight or curved, not angulate but rarely with small basal median angular projection 4
3. T6 of female with margin usually not denticulate[4], sometimes with lateral tooth, with median apical notch or emargination accommodating sting; T5 of female with basal edge of depressed marginal zone commonly obtusely angulate medially so that zone is broadly triangular; penis valves of male widely separated basally, united by long, narrow bridge; volsella projecting as lobe at apex of gonocoxite (widespread) ..... *Anthidium*
—T6 of female with margin denticulate, almost always without lateral tooth, usually without median apical notch; T5 of female with basal edge of depressed marginal zone not angulate medially; penis valves close together or fused basally, bridge therefore short or absent; volsella small or absent (Africa, southern Palearctic) ..... *Afranthidium* (part)
4. First recurrent vein joining first submarginal cell; axilla acutely pointed; face with longitudinal median shiny ridge from frons to clypeus (Africa) ..... *Serapista*
—First recurrent vein entering second submarginal cell; axillar margin rounded or straight; face without longitudinal median ridge 5
5. Basal area of propodeum hairless except laterally; pale markings absent on body; scutellum not angulate laterally; terga without impunctate margins (male unknown) (southern Africa) ..... *Anthidioma*
—Basal area of propodeum with hairs, sometimes very short; pale markings usually present, but if not, as in *Gnathanthidium* and *Afranthidium* (*Immanthidium*, etc.), then scutellum usually angulate laterally and terga with impunctate margins 6
6. Preoccipital ridge dorsally and omalus produced as translucent lamellae (Africa) ..... *Pachyanthidium* (part)
—Preoccipital ridge and omalus rounded or at most carinate, except preoccipital ridge lamellate in *Gnathanthidium* 7
7. Subantennal suture straight or weakly arcuate; S4 and S5 of male not strongly concave, rather simple, S3 to S5 without combs or areas of specialized bristles, their posterior margins straight or weakly concave (with lateral projections in *Neanthidium* and on S5 in *Gnathanthidium*) 8
—Subantennal suture distinctly arcuate outward; S3 to S5 of male usually concave, S4 and S5 or at least the latter short and largely hidden except in *Indanthidium*, at least S5 with posterior lateral projection except in *Pseudoanthidium (Exanthidium)* and *Indanthidium;* S3 often with comb or area of wavy bristles 10
8. T6 and T7 of male each with four large equidistant teeth; S4 and S5 of male with lateral projections; T6 of female with lateral spine and median emargination (length 9-13 mm) (north Africa) ..... *Neanthidium*
—T6 of male simple, T7 short, bidentate, bilobed, or tridentate; S4 and S5 without lateral projections or S5 with such projections in *Gnathanthidium;* T6 of female without or with very weak lateral spine and median emargination 9
9. Mandible of female with 13 or 14 teeth, apex broad, lower two teeth and upper one large, others small and subequal; scutellum transverse, truncate, carinate; tibiae coarsely tuberculate (east Africa) ..... *Gnathanthidium*
—Mandible of female with eight teeth or less; scutellum rounded as seen from above, not or incompletely carinate; tibiae not tuberculate except in some species of subgenera *Capanthidium* and *Xenanthidium* (Africa, southern Palearctic ..... *Afranthidium* (part)

---

[3] More anterior terga and T6 of males reflect the same features, often less clearly. Taxa that are not clearly separable by this character can be run to either alternative.
[4] T6 is denticulate in some, e.g., *Anthidium (Proanthidium) oblongatum* (Illiger).

10. T7 of male nearly as wide as T6, multidentate; subantennal suture arising at upper end of tentorial pit (S3 of male without wavy bristles; S5 with margin strongly concave but no lateral projections) (southern India) ..... *Indanthidium*
—T7 of male markedly narrower than T6, 2- or 3-toothed; subantennal suture arising from epistomal suture well above tentorial pit [except in *Pseudoanthidium (Royanthidium) reticulatum* Mocsáry] (Palearctic, Oriental, Africa) ..... *Pseudoanthidium*
11. Omalus lamellate, continued onto venter of thorax and there separated from middle coxa by less than width of middle trochanter 12
—Omalus lamellate or not, if lamellate often not continued onto venter of thorax, but if so, mesepisternum between mid coxa and omalus (however recognized) as wide as or wider than width of middle trochanter 13
12. Propodeum with fovea defined by carina behind spiracle; preoccipital ridge dorsally rounded or with low carina (Holarctic, Oriental, northern Australia, Africa) ..... *Anthidiellum* (part)
—Propodeum without fovea behind spiracle; preoccipital ridge behind vertex lamellate (Africa, southern Asia) ..... *Pachyanthidium* (part)
13. Lower part of preoccipital carina sloping forward and continuing directly to lower mandibular articulation; axilla frequently pointed posteriorly (anterior coxa with lamella in most species; hind trochanter of male with preapical ridge, carina, lamella or tooth on inner surface; arolia absent) (Palearctic, south to Kenya) .. *Icteranthidium*
—Lower part of preooccipital carina absent or if present and extending to lower part of head, ending below and mesal to lower mandibular articulation, or if reaching mandibular articulation [in *Anthidiellum (Chloranthidiellum)*], directed below it and then curving up to articulation; axilla not pointed posteriorly except in some parasitic genera that lack a scopa 14
14. Face with three longitudinal ridges or carinae, two juxtantennal carinae and median longitudinal one on frons and supraclypeal area that is often only a shiny ridge (body without yellow markings) 15
—Face without longitudinal median ridge or carina and usually without juxtantennal carinae 16
15. Mesepisternum in front of middle coxa with strong vertical ridge; scopa absent; scutellum produced as two broad, flat lobes overhanging metanotum and propodeum (Africa, Oriental, eastern Palearctic) ..... *Euaspis*
—Mesepisternum without vertical ridge in front of mid coxa; scopa present; scutellum rounded and not much produced in profile (west Africa) ..... *Atropium*
16. Vein cu-v of hind wing usually half as long as second abscissa of M+Cu or more, oblique; middle tibia as broad as hind tibia or nearly so (T7 of male simple or bilobed) 17
—Vein cu-v of hind wing less than half as long as second abscissa of M+Cu, oblique or transverse; middle tibia usually narrower than hind tibia 19
17. Claws of female simple (southern India) ..... *Trachusoides*
—Claws of female cleft or with inner median or preapical tooth 18
18. T7 of male curled under so that dorsal surface faces downward; mandible of female dull, minutely roughened and with very short hairs, carinae absent on basal half of mandible; middle tibia with anterior margin strongly curved so that at lowermost extremity it is usually at right angle to line across distal end of tibia (Holarctic, Africa, Oriental) ..... *Trachusa*
—T7 of male directed posteriorly although small, short and transverse; mandible of female slightly shining, carinae strongly shining; middle tibia with anterior margin less strongly convex, at apex at acute angle to line across apex of tibia (Oriental) ..... *Apianthidium*
19. Anterior part of axilla produced to a point or lobe directed laterally, behind which margin is concave; T7 of male with median point and two lobes on each side, thus with five apical projections (India) ..... *Acanthidium*
—Axilla rounded or sometimes pointed posteriorly, or if with basal lateral projection, it is curved posteriorly; margin of T7 of male with less than five apical projections 20
20. Axilla positioned and produced laterally so that it almost abuts against posterior end of tegula; arolia absent; scopa absent (Africa) ..... *Larinostelis*
—Axilla not abutting tegula; arolia present except in *Eoanthidium (Salemanthidium)*; scopa present except in *Stelis* and *Afrostelis* 21
21. Scopa present; front and middle tibiae each with one apical spine or angle except that *Cyphanthidium* and some *Eoanthidium* have two spines on middle tibia 22
—Scopa absent; front and middle tibiae each with midapical and posterior apical spine, so that each tibia has two apical spines 27
22. Juxtantennal carinae present although sometimes weak; interantennal distance usually less than, rarely equal to, antennocular distance; S6 of female usually with spine or premarginal ridge, sometimes weak and lateral only, so that sternal margin looks thick, sometimes elevated to lateral tooth (T7 of male over half as wide as T6) (Palearctic, Africa, Oriental) ..... *Eoanthidium*

—Juxtantennal carinae completely absent; interantennal distance usually greater than antennocular distance; S6 of female unmodified, with margin thin ..... .23

23. Scutoscutellar suture superficially similar to scutoaxillar suture, usually closed but if smooth shining floor of groove is visible, usually not divided into two parts; subantennal suture approximately straight or only slightly arcuate; fovea behind propodeal spiracle absent; body usually over 10 mm long, although *Cyphanthidium* may be 6.5 mm long ..... .24

—Scutoscutellar suture open to shiny bottom or fovea, thus very different from scutoaxillar suture, shiny area divided medially or *if* suture closed (as in *Anthidiellum* s. str.) *then* subantennal suture strongly arcuate outward; fovea behind propodeal spiracle present, defined posteriorly by carina, but fovea sometimes not larger than spiracle; body usually 8 mm long or less ..... .26

24. T6 of male with median apical tooth or small projection; body length 8.5 mm or less and metasoma with continuous yellow bands [form and coloration as in *Afranthidium (Oranthidium)*] (southern Africa) ..... *Cyphanthidium*

—T6 of male without median apical tooth; body length usually 8.5 mm or more, if less, as in some *Plesianthidium (Spinanthidium),* then metasoma without yellow ..... .25

25. Yellow or cream markings absent or limited to face of male; T3 and other terga with depressed premarginal zone sublaterally nearly half length of exposed part of tergum; T6 of male with median lobe (often subtruncate and elevated) and lateral tooth so that it is trifid or, in subgenus *Spinanthidiellum*, truncate with a longitudinal median ridge at apex (South Africa) ..... *Plesianthidium*

—Body with yellow or reddish-yellow markings; T3 and other terga with depressed premarginal zone sublaterally one-third length of exposed part of tergum or less; T6 of male simple or with short, broad, rounded median lobe, sometimes (in *Rhodanthidium* s. str.) also with lateral tooth and thus trifid (Palearctic) ..... *Rhodanthidium*

26. Omalar carina absent or extending down only to middle of mesepisternum; T7 of male, if trilobed, with median lobe much longer than lateral lobe or spine; subantennal suture straight (eastern Palearctic, Oriental) ..... *Bathanthidium*

—Omalar carina strong, sometimes lamellate, and extending onto ventral surface of thorax, sometimes across venter except in subgenus *Clypanthidium* in which omalar carina does not reach lower part of mesepisternum; T7 of male, if trilobed, with median lobe small, either not separated from lateral lobe by emargination or not longer than lateral lobe; subantennal suture usually arcuate outward (Holarctic, Oriental, northern Australia, Africa) ..... *Anthidiellum* (part)

27. Tegula enlarged, especially posteriorly, so that width posteriorly is nearly equal to length; scutum longer than wide (Africa) ..... *Afrostelis*

—Tegula of ordinary size and shape, widest medially and not as wide as long; scutum wider than long, only moderately so in subgenus *Stelidomorpha* (Oriental, Holarctic, south to Kenya) ..... *Stelis*

SUPPLEMENTARY KEY TO MALES OF ANTHIDIINE GENERA OF THE EASTERN HEMISPHERE

The preceding key will be frustrating for various reasons, but one major reason will be that Couplet 1 is largely based on a character of females; supplementary characters will help, but as indicated within the couplet, they are not always decisive. The following supplementary key for males leads either to certain genera or to couplets in the main key, thus bypassing Couplet 1. In reality, its main function is to help identify males of taxa that should run to 11 in the main key but that lack arolia, as do all taxa that run to 2.

A. Arolia absent ..... .B

—Arolia present ..... .11

B. Paleotropical species C

—Palearctic species 2

C. Vein cu-v of hind wing more than half as long as second abscissa of M+Cu, oblique; middle tibia as broad as hind tibia or nearly so ..... .D

—Vein cu-v of hind wing less than half as long as second abscissa of M+Cu; oblique or transverse; mid-tibia narrower than hind tibia ..... .E

D. T7 curled under so that dorsal surface faces downward; middle tibia with anterior margin strongly curved so that at lowermost extremity it is usually at right angle to line across distal end of tibia (Holarctic, Africa, Oriental) ..... *Trachusa* (part)

—T7 directed posteriorly although small, short, and transverse; middle tibia with anterior margin less strongly convex, at apex at acute angle to line across apex of tibia (Oriental) ..... *Apianthidium*

E. Axilla almost entirely lateral to lateral margin of scutum; outer, apical margins of fore and mid tibiae each with two minute spines (Kenya) ..... *Larinostelis*

—Axilla at most extending slightly lateral to lateral margin of scutum; outer apical margins of fore and mid tibiae each with at most one spine ..... F

F. Omalus carinate for at least three-fourths of distance from upper end to midventral line ..... G

—Omalus carinate for no more than half of distance from upper end to midventral line 2

G. Preoccipital carina present dorsally, behind vertex ..... H

—Preoccipital carina absent dorsally, behind vertex I

H. Hind tibia tuberculate on outer surface; scutellum very short, width greater than four times length, only slightly overhanging metanotum (for one-third its length) (east Africa) ..... *Gnathanthidium*

—Hind tibia not tuberculate; scutellum moderately long, width equal to or less than three times length, greatly overhanging metanotum (for one-half its length) (Africa, southern Asia) ..... *Pachyanthidium* (part)

I. Juxtantennal carinae present; T7 broadly truncate with small median projection (Palearctic, Africa, Oriental) ..... *Eoanthidium* (part)

—Juxtantennal carinae absent; T7 with three apical spines (Africa) ..... *Serapista*

COMMENTS, DESCRIPTIONS, AND KEYS TO SUBGENERA

The following pages consist of comments and descriptions justifying or explaining decisions made in preparing the List of Genus-Group Names. In addition, keys are given to the subgenera that we have recognized. Genera are arranged alphabetically to facilitate ready reference.

Acanthidium new genus

Type species: *Acanthidium batrae* Michener and Griswold, new species.

This is a genus having the body form of *Eoanthidium* or *Pseudoanthidium,* and conspicuous yellow markings. The basal part of the axilla is produced laterally and pointed, suggesting the shape of the axilla of some *Rhodanthidium (Asianthidium)* that led to the naming of *Axillanthidium* Pasteels, and likewise suggesting its shape in *Stelis (Malanthidium) malaccensis* (Friese). Thus this striking character has evidently arisen at least three times. If one ignores it, *Acanthidium* still does not fit into any other genus. The foveate scutoscutellar suture suggests *Eoanthidium* and *Bathanthidium.* From the first it differs by lack of juxtantennal carinae and the simple S6 of the female, among other features; from the latter it differs by the lack of the postspiracular fovea of the propodeum and the absence of the row of pits across the base of the propodeum. From all other genera *Acanthidium* differs in the short, broad T7 of the male with five apical projections, the lateral ones broadly rounded, the sublateral ones low, and the median one slender but blunt. Carinae are lacking on the head and thorax except for a carina on the pronotal lobe; the upper half of the omalus is sharply angular but not truly carinate. The scutellum is rounded posteriorly, not emarginate, rounded in profile, and scarcely overhanging the metanotum. Sterna of the male lack combs.

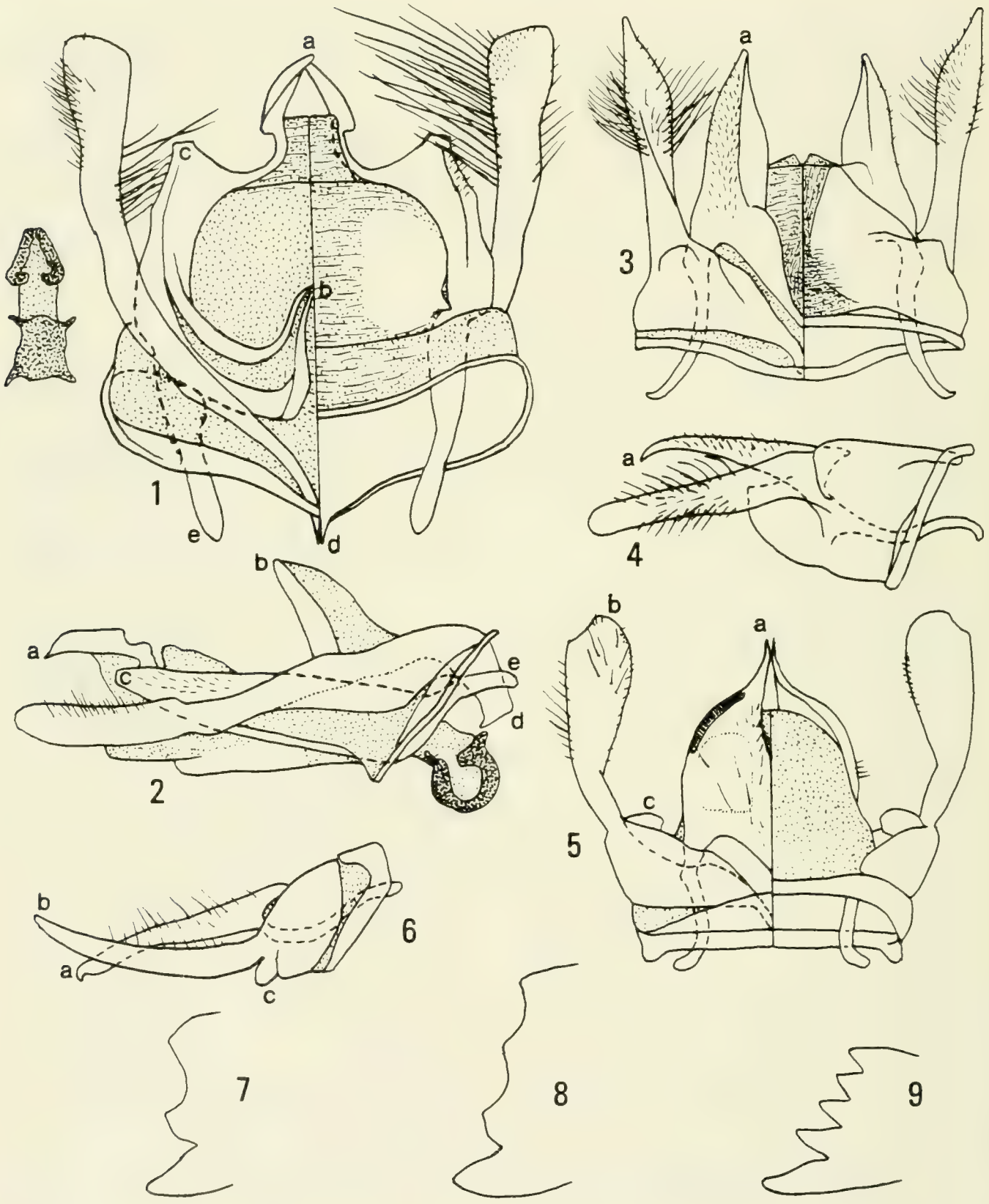
This genus occurs in India. The single known species is *A. batrae new species.*

Etymology: *Akanthos,* Greek, thorn, plus *Anthidium,* with reference to the basolateral projection of the axilla.

Acanthidium batrae new species

(Figs. 1, 2, 7, 8, 10-14)

MALE: Body length 7.5 to 8.0 mm; forewing length 6.0 mm; head width 2.8 mm. *Head:* Without carinae but preoccipital ridge behind vertex strongly angular. Clypeus nearly flat in profile, upper margin between subantennal sutures strongly convex; lower lateral margin short, reflexed; lower margin slightly concave, with three small dark denticles, not overhanging base of labrum. Mandible 3-toothed, interspaces between apices approximately equal, outer surface punctate, shining, with carinae evanescent in basal half. First segment of labial palpus slightly shorter than second; maxillary palpus longer than greatest width of galea, probably 4-segmented, second and third segments cylindrical, fourth (or apex of third) minute and tapering. Subantennal sutures straight, longer than diameter of antennal socket, parallel, lower ends arising from tentorial pits. Interantennal distance twice antennocular distance; ocellocipital distance equal to interocellar distance, about two-thirds of ocellocular distance. Genal area much narrower than eye seen from side, widest below middle of eye. Scape not reaching level of anterior margin of anterior ocellus; first flagellar segment nearly 1.5 times as long as broad, second slghtly broader than long, third about as broad as long, subsequent segments progressively a little longer so that tenth is conspicuously longer than broad, eleventh about 1.5 times as long as broad. *Thorax:* Without carinae except for strong carina on pronotal lobe; upper half of omalus sharply angulate but not quite carinate; front end of scutum gradually curved down, without smooth vertical surface; axilla with margin near base produced laterally as strong prominence behind which margin is concave; tegula widest medially; scutellum with posterior margin broadly convex seen from above, margin not carinate, laterally (along with axilla) overhanging, medially only slightly overhanging metanotum; scutoscutellar suture forming narrow fovea, weakly divided medially, fovea easily hidden by long hairs, pollen, etc. Propodeum without row of pits across base, laterally a doubtful indication of one or two small pits; fovea behind spiracle absent, possibly faintly indicated by ridge close behind spiracle; profile of propodeum convex, upper third declivous but not vertical, curving gradually to vertical lower two-thirds. Front and mid basitarsi each about as long as remaining tarsal segments together, hind basitarsus shorter than remaining segments; all basitarsi much shorter than tibiae; hind basitarsus less than three times as long as broad. Front and mid tibiae each with one apical spine; hind tibia with apex oblique, convex medially; tibial spurs strongly curved at apices. Arolia present. *Metasoma:* T2 widest. T1 with line margining basal concavity distinct only in middle third, horizontal surface more than half as long as vertical surface; T1 to T5 with posterior zones scarcely recognizable, feebly depressed, somewhat more so on T4 and T5; tergal graduli ending near spiracles except perhaps on T6 which has lateral longitudinal carina; T6 otherwise unmodified. T7


a
c
b
e
d
1
3
4
2
5
6
7
8
9

several times as wide as long, short, broad; lateral margin produced as rounded lamella that forms apicolateral lobe, median projection a blunt, black-tipped spine slightly exceeding lateral lobes; between spine and lateral lobe is weaker rounded projection; median third of dorsal surface of T7 with strong transverse ridge. S2 to S5 with posterior margins weakly and shallowly concave, marginal zones smooth, impunctate; S4 with strong longitudinal carina sublaterally; S6 with hairy lateral shoulder and broadly rounded, translucent midapical surface projecting somewhat beyond shoulders. *Punctation:* On head and thorax dense, contiguous throughout including propodeum, slightly less dense on metasoma, less dense and finer on legs; tibiae not at all tuberculate; apical depressed zones of T1 to T5 slightly more finely punctate than rest of terga. *Pubescence:* Rather abundant and long on head and thorax and base, sides and venter of metasoma, white, slightly dusky middorsally on metasoma; terga except laterally with hairs short, suberect; longer basitarsal hairs longer than diameters of basitarsi, but few such long hairs on hind basitarsus. *Integument:* Black with yellow markings as follows: mandible except for black apical margin and teeth, clypeus, paraocular area extending as stripe almost to summit of eye; gena completely below and extending as stripe across vertex behind ocelli, pronotal lobe, anterolateral mark and lateral stripe on scutum, axilla, medially interrupted marginal stripe on scutellum, quadrate mark on mesepisternum below pronotal lobe, irregular area on mesosternum, legs except blackish ventroapical areas on femora and most of ventral or inner surfaces of tibiae, broad transverse bands on T1 to T5 narrowly interrupted medially with semicircular midlateral posterior black intrusions into bands on T1 and T2; T6, T7, and sterna wholly yellow. Posterior margins of terga brownish, light brown on T5 and T6. Wings dusky, veins black.

FEMALE: Agrees with description of male except for usual sexual characters and as follows. *Head:* Lower margin of clypeus straight except for denticles which are as in male; mandible 4-toothed, upper two interspaces gently concave, outer surface finely punctate, especially apically, carinae distinct only on apical third. (Proboscis not examined.) Interantennal distance less than twice antennocular distance. First flagellar segment less than 1.5 times as long as broad, second almost twice as broad as long, following segments progressively longer but ninth still slightly broader than long and tenth about 1.5 times as broad as long. *Thorax:* Front basitarsus slightly longer than remaining tarsal segments together, other basitarsi about as long as remaining segments. *Metasoma:* T1 to T4 of about equal width. T6 without lateral carina, slightly concave in profile because of elevated apical area, margin with small midapical notch; S6 unmodified, slightly exceeding T6. *Pubescence:* On dorsum of head and thorax with intermixed dusky hairs; sides of metasoma without long hairs; scopa yellowish white; basitarsi with few hairs longer than diameters of basitarsi except lower margin of hind basitarsus with many such hairs. *Integument:* Frons below median ocellus with yellow mark; upper and posterior surfaces of femora with black areas; yellow bands of metasoma without midlateral black intrusions; S6 largely black.

Holotype male: INDIA: Uttar Pradesh: Mussoorie Lal Tibba, altitude 7500 feet (2308 m), June 23, 1965 (S. W. T. Batra), on "*Indigofera dosua* Buch.-Ham." Paratype male: Same data but July 1, 1965. Paratype female: Same data but June 25, 1965. These specimens are in the Snow Entomological Museum, University of Kansas, Lawrence, thanks to the generosity of Dr. S. W. T. Batra, after whom the species is named.

As indicated by Bingham's (1898) description and illustration and a specimen in the Natural History Museum, London, *Acanthidium batrae* resembles superficially in form and coloration *Anthidium desidiosum* Bingham, also from India. *A. batrae* is, however, smaller and entirely different in structure; for example, it has 4-toothed rather than 9-toothed mandibles in the female.

Genus *Afranthidium* Michener

This genus contains a large group of relatives of *Anthidium*, generally rather small and robust, with multidentate mandibles in the female as in *Anthidium*. Some species agree with *Anthidium* also in the depressed, medially widened premarginal zone of T5 (see key to genera for more details); the anterior margin of this zone, however, is not angulate as in *Anthidium*. In other species there is no such zone, and the impunctate marginal zone is sometimes broad, as in the subgenus *Immanthidium*. These and the other external characters indicated in the key to genera are generally distinctive but have exceptions. For example *Anthidium (Proanthidium) oblongatum* (Illiger) has T6 of the female denticulate, without a lateral tooth, and with a small midapical notch, thus combining the usual features of *Anthidium* and *Afranthidium*. The wide separation of the penis valves of *Anthidium* and the long bridge between their bases is the only known invariably good character that distinguishes *Anthidium* from *Afranthidium*.

Afranthidium contains diverse elements and one could justify dividing it into several genera. Until a proper analysis is made, we have not done so. The subgenera *Immanthidium*, *Nigranthidium*, and *Zosteranthidium* are particularly distinctive.

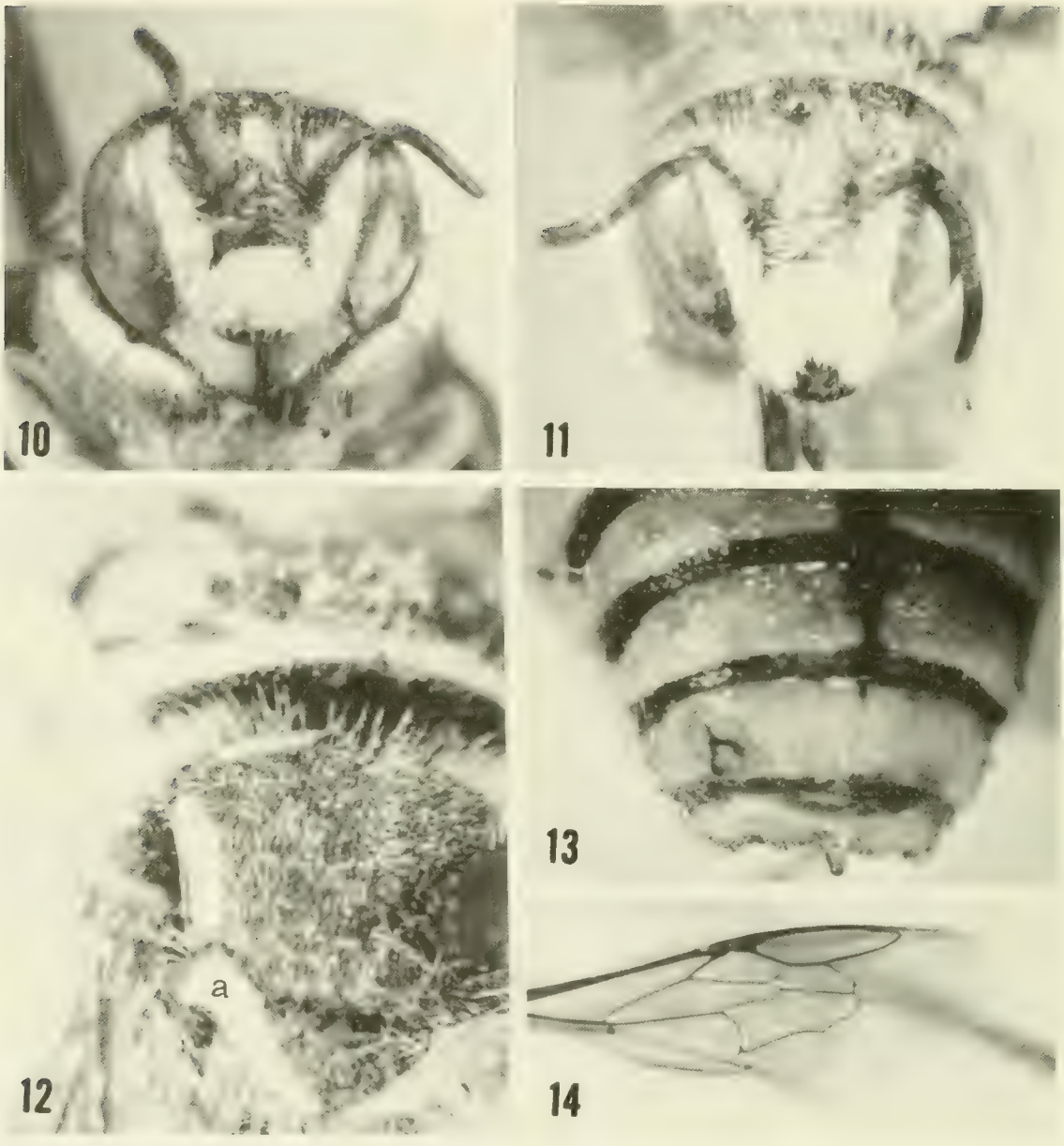
Key to the Subgenera of *Afranthidium*

1. Margins of T2 to T5 broadly impunctate, median lengths of impunctate zones usually one-sixth length of exposed parts of terga or more, margins transparent, pale brown or cream colored; male gonostylus enormous, broad, flat, and almost membranous; pronotal lobe not carinate, sometimes with small punctate and hairy ridge in position of carina . . . . . *Immanthidium*

—Margins of T2 to T5 punctate or narrowly impunctate, median lengths of impunctate zones about one-seventh lengths of exposed parts of terga or less, margins dark or translucent brownish; male gonostylus not broad, flat and almost membranous al-

← **Figs. 1-6.** Genitalia of males, dorsal-ventral and lateral views; in the former, dorsal views are at the left, ventral at the right. Letters identify same structures for any one species, e.g., a in a dorsal view is the same as a in a lateral view. **1, 2.** *Acanthidium batrae* Michener and Griswold; sclerotization that may be in the basal part of the endophallus is shown at left in dorsal view, and at lower right of Fig. 2, in lateral view. **3, 4.** *Indanthidium crenulaticauda* Michener and Griswold. **5, 6.** *Pseudoanthidium (Tuberanthidium) bracheatum* Michener and Griswold.

Figs. 7-9. Apices of mandibles. **7.** *Acanthidium batrae* Michener and Griswold, male. **8.** Same, female. **9.** *Indanthidium crenulaticauda* Michener and Griswold, male.



Figs. 10-14. *Acanthidium batrae* Michener and Griswold. **10.** Face, female. **11.** Face, male. **12.** Slightly lateral view of dorsum of thorax, male, to show shape of axilla (a). **13.** Metasomal apex, male, slightly lateral view to show two convexities lateral to median spine of T7. **14.** Forewing, male.

though sometimes broadly paddle-shaped; pronotal lobe usually with transverse carina or low lamella which is hairless even when it extends only partway across lobe 2

2. Scutellum rounded in profile, not or scarcely overhanging metanotum, even laterally axilla and scutellum not much overhanging; outer surfaces of tibiae not more coarsely punctate than mesepisternum, not tuberculate 3

—Scutellum acute, right angular or sometimes rounded in profile, medially often strongly overhanging metanotum; laterally scutellum and usually axilla overhanging large fossa and usually acute or narrowly rounded as seen obliquely to show profile of lateral part of scutellum and of axilla; outer surfaces of tibiae, especially of female, coarsely, irregularly punctate, sometimes with extensive smooth areas between punctures, these punctures commonly coarser than those of mesepisternum, tibial surfaces usually tuberculate, not or weakly so in *Capanthidium* and *Mesanthidium* 7

3. T2 to T5 with apical bands, broken medially, of

white plumose hair; propodeal triangle with punctures (and hairs) widely separated from one another, surface between punctures strongly shagreened, dull; body and legs black, without pale markings ..... *Zosteranthidium*

—T2 to T5 without apical hair bands [except for *Afranthidium murinum* (Pasteels)]; propodeal triangle rather densely punctate and hairy, surface between punctures shining; body and legs usually with yellow or white markings, but if not, then at least anterior surfaces of front and mid tibiae brownish yellow 4

4. Hind basitarsus of female with apical projection over base of second tarsal segment; hind trochanter of male with apicoventral denticle; sterna of male with distinct basal fasciae arising at graduli; body black, yellow or cream color usually limited to minute streak along inner margin of eye of both sexes ..... *Nigranthidium*

—Hind basitarsus of female with apex truncate, without apical projection; hind trochanter of male without apicoventral denticle; sterna of male without basal fasciae; body with yellow or cream colored areas at least on face of male and metasomal terga 5

5. T5 of female without lateral spine; T1 of female with carina separating anterior from dorsal surfaces abruptly strengthened laterally and thence extended lateroposteriorly; apex of T7 of male with two lobes, each two or three times as broad as long, emargination between them with small median spine; S6 of male with small, pointed midapical process at base of which are two spines directed forward ..... *Domanthidium*

—T5 of female with lateral spine; T1 carina of female unmodified; apex of T7 of male 2-lobed, usually with median angle or tooth, or trifid, lateral lobes about as long as broad or longer; S6 of male without small apical process and spines 6

6. Gonostylus of male tapering, not or scarcely longer than gonocoxite, not attaining middle of penis valve; ventral surface of mesepisternum of female covered with strong, backward directed, golden to black bristles that appear flattened, minutely barbed, and blunt or abruptly tapered at apices (S6 of male elongate, produced to narrowly rounded or bidentate apex) ..... *Oranthidium*

—Gonostylus of male expanded apically, about twice as long as gonocoxite, attaining apex of penis valve or nearly so; ventral surface of mesepisternum of female with pale, gradually tapering hairs similar to those of adjacent areas ..... *Afranthidium* s. str.

7. Posterior margins of metasomal terga not curved upward, lying near surfaces of following terga; axilla extending laterally beyond scutal margin; male gonostylus greatly reduced, attaining about middle of penis valves, which are completely fused to one another (palearctic) ..... *Mesanthidium*

—Posterior margins of at least some metasomal terga, seen in profile, curved upward away from following terga; axilla not extending laterally beyond scutum except in some *Branthidium;* male gonostylus reaching to or beyond level of apical fourth of length of penis valve 8

8. T6 of female with preapical denticulate ridge parallel to denticulate apical margin (scutellum distinctly carinate except for small midapical emargination) (male unknown) ..... *Xenanthidium*

—T6 of female without preapical denticulate ridge 9

9. T6 of male with preapical usually denticulate transverse ridge at least laterally; tibiae coarsely punctate but not or weakly tuberculate on outer surfaces ..... *Capanthidium*

—T6 of male without preapical ridge; tibiae strongly tuberculate on outer surfaces 10

10. Preoccipital carina present laterally; male S3 with trapezoidal apical projection; T5 and T6 of male with lobate lateral carinae; female T5 and T6 with lateral longitudinal carinae ..... *Mesanthidiellum*

—Preoccipital carina absent; male S3 margin not produced; T5 (usually) and T6 without lateral carinae in either sex ..... *Branthidium*

Subgenus *Afranthidium* Michener s. str.

The species described as *Anthidioma murinum* Pasteels (1984) is not closely related to *Anthidioma* and appears to belong to the genus *Afranthidium,* but does not completely fit the characterization of any recognized subgenus. As the species is known only in the female, a firm decision as to its placement is premature. The pronotal lobe lacks a carina but in other respects *murinum* runs to couplet 3 in the key to genera, or to *Afranthidium* s. str. if its tergal hair bands are ignored. It differs from *Afranthidium* s. str. in the absence of lateral metasomal spines although T3 to T5 have small lateral lobes, and from *Zosteranthidium* in the presence of yellow maculations and other characters. *Afranthidium murinum* (Pasteels) (new combination) is unusual in its abundant white hair, which forms dense apical tergal bands on the metasoma, suggesting *Zosteranthidium.* The species is known only from Namibia. In addition to the type specimen, two additional females from approximately the type locality (Pomona, in Diamond Area No. 1, Namibia) were taken on flowers of a yellow legume by V. B. Whitehead and are in the South African Museum, Capetown.

Subgenus *Branthidium* Pasteels

Honanthidium Pasteels (1969a) was described as near *Tuberanthidium* (here considered a subgenus of *Pseudoanthidium)* and was later synonymized with *Tuberanthidium* (Pasteels, 1984). It is known only in the female, so its place is not readily determined with certainty. However, it seems to us much more likely to be an *Afranthidium,* closest to the subgenus *Branthidium,* to which it runs in the key to subgenera,

because of the strongly denticulate (and not emarginate) T6 of the female, the presence of weak swellings at the sides of T2 to T5 (these could represent spines of the male; they are not present in females of *Pseudoanthidium*) and the rather narrow, unbroken yellow bands of the metasomal terga. Unusual features are the swollen head, with the genal area broader than the eye, and the strong and elevated trimmal carina extending from the mandibular acetabulum to the fourth mandibular tooth. This is probably not homologous to the swelling in the same region, but without a carina, found in *Tuberanthidium*. The fifth (small) and sixth (uppermost) mandibular teeth are depressed, so that *Afranthidium (Branthidium) honestum* (Cockerell) (new combination) runs with difficulty to the multidentate part of the key to genera unless the mandibles are opened. Teeth two to four, however, are of more or less equal size, separated by narrow notches as shown by Pasteels (1969a, fig. 82); somehow a tooth was subsequently lost in Pasteels' (1984, fig. 124) later drawing.

Afranthidium (Branthidium) guillarmodi (Mavromoustakis) as identified by Pasteels is unusual in having the axilla extending laterally as in the subgenus *Mesanthidium* and T5 (also T3 and T4 but not T6) with a lateral, almost carinate lobe in the female, suggesting *Mesanthidiellum* which has such carinae on T5 and T6.

Subgenus *Capanthidium* Pasteels

Type species: *Anthidium "capicola* Friese," lapsus for *capucola* Brauns, 1905, by original designation. Pasteels (1969a) twice rendered the specific name *capucole*, once *capicola*, and each time attributed it to Friese, in whose paper Brauns' species was published.

This subgenus includes certain palearctic species, at least *A. (C.) naefi* (Benoist) and *schulthessii* (Friese), formerly placed in the subgenus *Mesanthidium*. The male genitalia of the seven or more additional palearctic species placed in *Mesanthidium* by Pasteels (1969a) presumably provide the most reliable basis for placing these species in *Mesanthidium* (with very reduced gonostyli, see key to subgenera) or *Capanthidium*.

Subgenus *Mesanthidiellum* Pasteels

One of us (CDM) would consider this a synonym of *Branthidium*.

Subgenus *Nigranthidium* Pasteels

Pasteels (1984) included two species, *A. (N.) concolor* (Friese), of which *Osmia willowmorensis* Brauns was considered a synonym, and *A. tergofasciatum* (Pasteels). The synonymy of *O. willowmorensis* is incorrect. It thus forms the new combination *A. (N.) willowmorense* (Brauns). *A. tergofasciatum* (Pasteels) is transferred to the subgenus *Zosteranthidium*.

Subgenus *Xenanthidium* Pasteels

Xenanthidium should probably be considered a synonym of *Capanthidium*, but since it is known only from a single female specimen that has rather distinctive characters, it seems premature to synonymize it.

A large folded label on the type specimen of *X. biserratum* Pasteels (Natural History Museum, London) provides much better data than did Pasteels (1984) in print. Combining this folded label with the label that Pasteels read, the type is from Pouss on the Logone River in north Cameroon, 200 miles south of Lake Chad, 250 m [altitude?], November, 1979 (G. Popov).

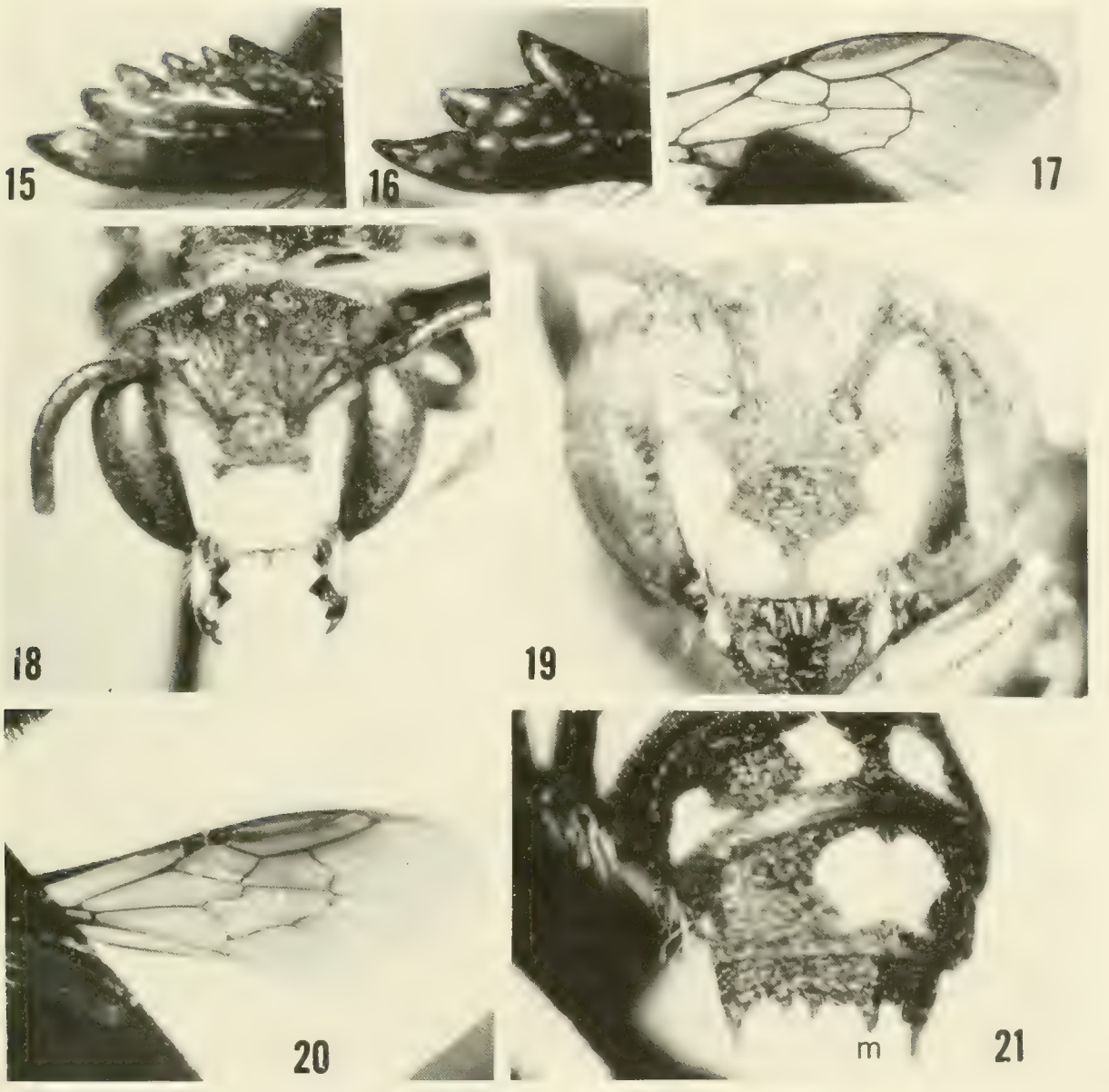
Zosteranthidium new subgenus

(Figs. 15-17)

Type species: *Nigranthidium tergofasciatum* Pasteels, 1984.

Although the type species of *Zosteranthidium* was placed in *Nigranthidium* by Pasteels (1984), it is not closely related to that subgenus. Its somewhat elongate body, pale tergal hair bands suggesting *Afranthidium murinum* Pasteels (see discussion of *Afranthidium* s. str.), and complete absence of yellow or white integumental markings, as well as its size (body length 9 to 10 mm), result in a species that exactly resembles some species of *Hoplitis* (Osmiini). Its distinctive features are as follows:

Maxillary palpus as long as width of maxilla at point of palpal attachment, second segment about seven times as long as wide, widest near base, tapering, bristly (thus maxillary palpus longer than in any other *Afranthidium*); labial palpus with second segment about twice as long as first, third segment broadly attached to second and continued in same direction, only fourth directed laterally. Mandible of female 6-toothed, teeth 2 and 6 subequal, 5 smallest, teeth 4 and 5 a little shorter than the others but apices of all teeth nearing the same line; mandible of male 3-toothed. Clypeal apex denticulate in female. Second recurrent vein slightly beyond second transverse cubital; stigma with distal half tapering into marginal cell. Scutellum rounded posteriorly, not at all overhanging; propodeum strongly shagreened, punctures on triangle dispersed, almost absent in median zone and lower part of triangle, hairs correspondingly sparse. Hind basitarsus with apex truncate, not produced as in *Nigranthidium*. T2 to T5 with preapical bands of white plumose hairs, broken middorsally; T5 with posterior premarginal zone depressed but not sharply defined, somewhat more finely punctate than rest of tergum, anterior margin of zone not angulate medially (so poorly defined that angle might not be visible), narrowed laterally but more than half of median width, impunctate tergal margin black, broader than base of last hind tarsal segment; T6 of female without preapical carina, profile straight, reflexed lateral portion smaller than in related bees, exposed reflexed area being about as long as distance from distal end of area to small midapical tergal notch, thus about half as long as in other *Afranthidium*. T6 of male with lateral tooth; T7 of male not strongly exserted, with broad emargination between two teeth as illustrated by Pasteels (1984). Metasomal sterna more modified than in other *Afranthidium;* S2 and S3 with preapical zones of very long white hairs, S3 with midapical area of stiff, straight hairs; S4 with large midapical area of stiff, straight, brown hairs; S5 concave, with small lateral tubercle or tooth, posterior part shining and hairless except posterior marginal band of short straight brown hairs on lateral third of



Figs. 15-17. *Afranthidium (Zosteranthidium) tergofasciatum* (Pasteels). **15.** Mandible, male. **16.** Mandible, female. **17.** Portion of forewing, female.

Figs. 18-21. *Indanthidium crenulaticauda* Michener and Griswold. **18.** Face, male. **19.** Face, female. **20.** Forewing, male. **21.** Metasomal apex, male, slightly lateral view to show teeth of T7 lateral to median spine (m).

sternum; S6 broad, shining, largely impunctate and hairless, with strong lateral gibbosity, posterior margin thin, broadly convex; S7 broad with apical projection margined by hairs [this shape is illustrated by Pasteels (1984, fig. 114) as S6]. Gonostylus slender, about shape shown by Pasteels (1984) but with several large curved hairs arising on upper and inner surfaces; penis valve with apex bent upward and subtruncate.

This taxon is so distinctive that it could well receive generic status. It does appear to be nearest to *Afranthidium*, and for the present is included. As indicated elsewhere, the status of *Afranthidium* is considered tentative, for it contains rather diverse forms. In the difficult couplet 2 of the key to genera, *Zosteranthidium* runs to 4 because the premarginal zone of T5 is poorly defined, not greatly narrowed laterally, its anterior margin not angulate, and the smooth posterior margin relatively broad.

Zosteranthidium contains a single species, *Afranthidium (Zosteranthidium) tergofasciatum* (Pasteels), new combination, from western Cape Province, South Africa.

Etymology: *Zoster*, Greek, belt, with reference to the metasomal hair bands, plus *Anthidium*.

Genus *Afrostelis* Cockerell

The two spines on front and middle tibiae and other characters indicate that this genus is closely related to *Stelis;* it might be merely a specialized derivitive of *Stelis* not warranting generic rank. However, the male gonostylar form (slender, straight, and minutely capitate) is probably more primitive than that of any *Stelis*. That fact and the striking thoracic characters lead us to recognize *Afrostelis* as a genus.

Genus *Anthidiellum* Cockerell

Key to the Subgenera of *Anthidiellum*

1. Postgradular parts of T2 to T5 of females and to T6 of males swollen laterally so that from above sides of metasoma seem lobed; S5 of male without comb; mandible of female with preapical shoulder on lower margin, below lower tooth (Holarctic) ..... *Anthidiellum* s. str.
—Terga not swollen laterally; S5 of male with margin broadly concave and armed with comb of black teeth, at least laterally (male unknown in *Ananthidiellum*); mandible of female without preapical shoulder on lower margin (eastern hemisphere) 2
2. Mandible of female minutely sculptured, dull, almost without carinae, apex expanded, 1.5 times as wide as basal width; subantennal suture straight; T1 to T4 without pale markings (southeast Asia) ..... *Ananthidiellum*
—Mandible of female somewhat shining, often coarsely punctate, somewhat dull distally in *Ranthidiellum* and *Clypanthidium,* with carinae, apex but little wider than base except in *Ranthidiellum;* subantennal suture arcuate [scarcely so in *A. (Anthidiellum) breviusculum* (Pérez); not clearly recognizable and perhaps not arcuate in *A. [Clypanthidium bimaculatum* (Friese)]; T1 to T4 with yellow, cream, or reddish bands except in subgenus *Clypanthidium* and some *Ranthidiellum* 3
3. Preoccipital carina present at sides, behind eyes, but absent behind vertex; lamella on pronotal lobe tapering but extending nearly as far mesad from lateral margin of scutum as laterad; axilla extending laterally beyond margin of scutum (basal zone of propodeum laterally horizontal with well-developed pits) (east Africa) ..... *Chloranthidiellum*
—Preoccipital carina complete, present only behind vertex or absent; pronotal lobe with lamella or carina usually extending little mesad from lateral margin of scutum; axilla not extending laterally beyond lateral margin of scutum 4
4. Tegula narrowly rounded posteriorly; omalar carina reaching about halfway down omalus (southeast Asia) ..... *Clypanthidium*
—Tegula broadly rounded or almost transverse posteriorly; omalar carina extending to venter, or in some *Pycnanthidium* very weak or perhaps absent on lower half of mesepisternum 5
5. T1 with carina separating anterior and dorsal surfaces; apex of mandible but little wider than base; body black with yellow or cream markings on all tagmata (Africa, southern Orient, northern Australia) ..... *Pycnanthidium*
—T1 without carina between anterior and dorsal surfaces; apex of mandible of female about 1.5 times as wide as base; body brown with red markings or yellowish and black but without yellow on T1 to T4 (southeast Asia, Indonesia) ..... *Ranthidiellum*

Subgenus *Clypanthidium* Pasteels

Discovery of the male of this subgenus might show that it is out of place in *Anthidiellum.* The *Anthidiellum*-like features of *Clypanthidium,* by which it differs from *Bathanthidium* where it was placed by Pasteels (1968, 1969a), include (1) the presence of a carina on the upper half or more of the omalus (it extends farther down in other *Anthidiellum*), (2) the enlarged scutellum, strongly overhanging the metanotum (but it is not sharply angled, carinate or lamellate apically, as in other *Anthidiellum*), (3) the rather abrupt line between the area with keirotrichia and that with other hairs along the upper margin of the hind tibia (but it is not so abrupt as in other *Anthidiellum*), (4) the robust hind basitarsus (it is about three times as long as wide, about as in *Anthidiellum,* but is over four times as long as wide in *Bathanthidium*) and (5) the robust body form.

Subgenus *Pycnanthidium* Krombein

The name *Pygnanthidiellum* was proposed for the African species and contrasted to the Indoaustralian species. In the latter group the hind tibia and basitarsus are finely punctate, the omalar carina is weak or absent below, and the pronotal lobe is carinate or weakly lamellate. In the African group the hind tibia and basitarsus are coarsely punctate, the omalar carina is complete and the pronotal lobe sometimes strongly lamellate. Also in the African group the hind basitarsus of the female is enlarged, nearly as wide as the tibia. It now appears that both groups occur in Sri Lanka, India and Burma (Pasteels, 1972). We do not regard the differences between these groups as justification for subgeneric distinction.

Subgenus *Ranthidiellum* Pasteels

Pasteels designated the type species as *"Anthidium rufomaculatum"* Cameron, and on p. 123 he described it, including the reference "Cameron, 1897, Mem. Manchester Soc., 41." Cameron published in 1897 in vol. 41 of that journal, but *Anthidium rufomaculatum* does not appear there.

It is not the same as *Anthidium rufomaculatum* Friese, 1899, from Syria. There is, however, *Protoanthidium rufomaculatum* Cameron, 1902 (Jour. Straits Branch, Royal Asiatic Society, no. 37) that agrees reasonably well with Pasteels' description. No doubt this is the species that Pasteels intended as the type species of *Ranthidiellum.*

An alternative way of looking at the type species of *Ranthidiellum* is to list it as *Anthidiellum rufomaculatum* Pasteels, 1969, by original designation, recognizing that his attribution of the name to Cameron (and the reference) were errors. Pasteels described the species in full, as though it were new. *Anthidiellum rufomaculatum* Pasteels, 1969, seems to be a synonym of, as well as a junior secondary homonym of, *Protoanthidium rufomaculatum* Cameron, 1902. Thus ultimately the type species of *Ranthidiellum* is the same as is indicated in the preceding paragraph.

Genus *Anthidioma* Pasteels

In the absence of males, the true position of *Anthidioma* is not clear; for the present its generic rank is maintained.

Pasteels (1984) included two species, each then known from a single female specimen, in *Anthidioma.* One of them, *A. murina* Pasteels, is an *Afranthidium;* see the discussion under *Afranthidium* s. str. One additional female of an *Anthidioma* species related to but different from *A. chalicodomoides* Pasteels has come to hand.

Genus *Anthidium* Fabricius

The distinctions between *Anthidium* and the remaining genera (as a group) with tapering mandibular teeth in the female are rather subtle and tend to break down among probably derived subgenera that seem to have lost one or another of the characters of the genus. The combination of characters remains distinctive, however. In *Anthidium* the subantennal suture is usually straight. T6 of the female has an apical depressed rim, usually smooth and shining, often hidden by hairs, and sometimes unrecognizable. This rim and usually the tergum as a whole have a median apical notch or emargination, sometimes small or largely hidden by hairs, but sometimes large and conspicuous, especially in the subgenus *Callanthidium.* Laterally, T6 of the female nearly always has a tooth, angle, or shoulder, mesal to which there is an emargination, sometimes very weak. In the subgenus *Proanthidium* the lateral emargination and tooth are absent but the impressed margin and notch are present medially. T1-T5 of females and T1-T6 of males have narrow, smooth apical margins of uniform width, usually flat or nearly so. Anterior to each margin but behind the elevated mid-tergal zone (often distinct only laterally) is the depressed marginal zone, differentiated (commonly by finer and closer punctation) from the rest of the tergum. Problems with this character are found, among others, in *A. (Nivanthidium) niveocinctum* Gerstaecker from Africa, which has the depressed zone of T5 of the female sparsely punctate medially, but laterally it is as described. In *A. (Severanthidium) severini* Vachal, also from Africa, the punctures of the depressed zone are sparse and shallow and this zone merges into the smooth margin; the shape of the depressed zone, however, is as in other *Anthidium.* The preapical depressed zones are wider (at least on T5) medially than laterally; this is usually evident even when the zone is not well differentiated medially. The anterior margin of the preapical zone is usually angled medially so that the whole zone is a very broad triangle. These characters of the tergal margins are best examined on T5 of both sexes, but are often evident on more anterior terga. In the other genera with similar female mandibles, the smooth apical tergal margins are usually convex and the preapical zones are not recognizable except laterally or are scarcely wider medially than laterally. In some species of the subgenus *Proanthidium* the marginal zones are also convex.

Key to the Old World Subgenera of *Anthidium*

1. Scutellum rounded in profile, not carinate or lamellate, not greatly overhanging metanotum and propodeum; pronotal lobe with or without carina (Holarctic, Oriental, Africa) ..... *Anthidium* s. str.
—Scutellum angulate in profile (at least as seen obliquely to show profile of lateral part of scutellum), strongly carinate or lamellate at least laterally, greatly overhanging metanotum and propodeum; pronotal lobe carinate or lamellate 2
2. Pronotal lobe carinate; axillar suture weak; scutoscutellar suture not in deep depression so that scutellum nearly continues profile of scutum (scutellum strongly produced posteriorly as rather flat structure ending in lamella) (east Africa) ..... *Nivanthidium*
—Pronotal lobe with more or less anteriorly directed or erect, translucent lamella; axillar suture strong; scutoscutellar suture in depression so that scutellum is independently convex in profile 3
3. Scutellum ending in lamella or large carina almost all the way across; hind basitarsus with longitudinal carina on outer surface; omalus sharply angulate or weakly carinate 4
—Scutellar margin with broad median part neither carinate nor lamellate; hind basitarsus not carinate; omalus rounded or forming rounded angle (Palearctic) 5
4. Posterior scutellar margin seen from above subtruncate, its lateral part curved forward becoming more or less longitudinal; antennae below level of middles of eyes which converge strongly below so that clypeus is unusually small (Africa, Arabian Peninsula) ..... *Severanthidium*
—Posterior scutellar margin seen from above broadly rounded with small median emargination, laterally oblique, only at extreme end next to axilla some-

times becoming longitudinal; antennae near level of middles of eyes which converge slightly to moderately (xeric southern Palearctic) ..... *Gulanthidium*

5. Scutellum seen from above with margin curved forward at each side to axillar margin; hind basitarsus of female less than four times as long as broad (central Asia) ..... *Turkanthidium*

—Scutellum seen from above with margin more or less transverse, curved forward rather abruptly or angled forward at side to axillar margin, scutellar margin often with lateral angle protruding posteriorly; hind basitarsus of female four or more times as long as broad (Palearctic) ..... *Proanthidium*

Subgenus *Anthidium* Fabricius s. str.

This is a large and rather diverse subgenus. Unusual species or small groups have been given subgeneric or generic names, but such names seem unnecessary, being apparently based on species derived from among the "ordinary" species of *Anthidium* s. str.

The name *Ardenthidium* has been applied to a group of unrelated species having about ten mandibular teeth in the female, compared to five to seven in most other species. In other respects the type species, *A. ardens* Smith, and the quite dissimilar *A. undulatiforme* Friese appear to be *Anthidium* s. str. *A. echinatum* Klug, the type species of *Echinanthidium*, is perhaps better differentiated from most other *Anthidium* s. str. It is one of the few palearctic forms without a hind tibial carina. The clypeal margin of the female is not thickened as in most *Anthidium* s. str. In this respect it resembles *Turkanthidium* and most *Proanthidium*. Like many desert bees (Morocco to Pakistan), the species placed in *Echinanthidium* have a pallid aspect due to the largely yellow metasoma with preapical tergal fringes of dense white hairs. *A. pontis* Cockerell *(Pontanthidium)* differs from other *Anthidium* s. str. in the protuberant clypeus, a character that alone seems not to justify subgeneric recognition.

Genus *Bathanthidium* Mavromoustakis

This genus contains three taxa that have genus-group names. Because only four species are involved, it may seem unreasonable to recognize subgenera. We have done so partly because there is no assurance that the genus is monophyletic. The subgenera *Bathanthidium* s. str. and *Stenanthidiellum* are slender bodied, quite clearly close relatives; e.g., both have a small median comb on S4 of the male. The subgenus *Manthidium* is more robust, resembling *Anthidiellum* subgenus *Ranthidiellum*. All three subgenera have a comb on S5 of the male occupying almost the entire width of the segment.

Key to the Subgenera of *Bathanthidium*

1. Fovea behind propodeal spiracle rounded, delimited by strong carina; T7 of male trilobed, median lobe longest (upper margin of propodeum without row of pits except laterally) (southern China, Taiwan) ..... *Bathanthidium* s. str.

—Fovea behind propodeal spiracle elongate, weakly delimited; T7 of male simple or with slightly produced median lobe 2

2. Basal zone of propodeum not distinct, with irregular, sculptured, sloping pits laterally; T6 of male with elevated median section and concave lateral sections (Oriental) ..... *Manthidium*

—Basal zone of propodeum distinct laterally with regular, shiny, nearly horizontal pits; T6 of male with surface convex (northeastern Asia) ... *Stenanthidiellum*

Subgenus *Stenanthidiellum* Pasteels

Romankova (1988) considers the type species of *Stenanthidiellum* and *Lasanthidium* (listed above as a probable junior synonym of *Stenanthidiellum*) to be in different genera. The identity of *Anthidium sibiricum* Eversmann (type species of *Stenanthidiellum*) may be uncertain. The genitalia of *Stelis malaisei* Popov (type species of *Lasanthidium)* are similar to those of *Bathanthidium (Bathanthidium) bifoveolatum* Alfken (see Popov, 1941) and it may be that *Bathanthidium* and *Stenanthidiellum* should be united.

Genus *Benanthis* Pasteels

This genus, known from a Malagasy specimen that has apparently been misplaced or lost, is unknown to us. Pasteels (1969a, 1984) described and sketched parts of the specimen. We cannot comment on its probable relationships.

Genus *Cyphanthidium* Pasteels

Two species were placed in separate genera *(Cyphanthidium* and *Trianthidiellum)* by Pasteels (1969a); Pasteels (1984) transferred *Trianthidiellum* to *Anthidiellum* as a subgenus, perhaps because of the arcuate subantennal sutures. However, in specimens of *"Trianthidiellum"* near *C. sheppardi* (Mavromoustakis) (type species of *Trianthidiellum*) (National Collection of Insects, Pretoria, South Africa) they are straight, and in *C. sheppardi* they are only slightly arcuate; Pasteels' figure (1984, fig. 240) shows the suture curved on one side but nearly straight on the other. Mavromoustakis (1937) described *C. sheppardi* as lacking arolia but they are present although rather small in the type specimen as well as in other specimens that we have seen. Thus there seems to be no justification for two genus-group names for the two described species.

Genus *Eoanthidium* Popov

Key to the Subgenera of *Eoanthidium*

1. Subantennal suture straight; inner surface of hind tibia curving onto upper margin without sharp line between keirotrichiate area and region of longer hairs (arolia present; scutoscutellar suture closed,

similar to scutoaxillar suture; T4 to T6 of female and T5 and T6 of male with small lateral spines) (southern India) ..... *Hemidiellum*

—Subantennal suture strongly arcuate outward; inner surface of hind tibia flat, keiotrichiate area ending abruptly at sharp line, often carinate, along upper margin of tibia 2

2. Arolia absent; profile of T6 of female convex; T4 to T6 with lateral spines (scutoscutellar suture closed, similar to scutoaxillar suture) ..... *Salemanthidium*

—Arolia present; profile of T6 of female concave (convex distally in subgenus *Clistanthidium*); T4 and T5 without lateral spines 3

3. Front coxa with strong carina or lamella transverse to axis of body or extended distally and thus largely longitudinal; S6 of female not thickened apically, without lateral carina or spine; T6 of male with lateral tooth; scutoscutellar suture not very different from scutoaxillar suture, or in *E. (C.) nasicum* (Friese) foveate nearly as broadly as in *E. (Eoanthidium)* s. str. ..... *Clistanthidium*

—Front coxa without strong carina or lamella; S6 of female thickened apically, with lateral carina or spine; T6 of male without lateral tooth; scutoscutellar suture open with shiny impunctate floor divided medially to form two foveae ..... *Eoanthisium* s. str.

Clistanthidium new subgenus

Type species: *Dianthidium turnericum* Mavromoustakis, 1934.

The species of this subgenus were placed in *Eoanthidium* (as a subgenus of *Anthidiellum*) by Pasteels (1984). *Clistanthidium* differs from *Eoanthidium* s. str., however, in several characters that suggest a separate subgeneric status. It is more robust, having the body form of a *Dianthidium*. It differs from *Eoanthidium* s. str. in the presence of two blunt spines or a single broad bilobed spine at the apex of the middle tibia, although this condition is approached in *E. (Eoanthidium) clypeare* (Morawitz), and in the simple margin of S6 of the female, not at all thickened, although S6 has a median keel ending in a preapical, median spine. *Clistanthidium* seems to be most similar to *Eoanthidium* s. str. from which it differs as follows.

Juxtantennal carina well developed, ocelloccipital distance less than ocellocular and interocellar distances, omalar carina (which extends onto thoracic venter but does not approach midline) elevated to form low lamella on upper half of mesepisternum; carina of pronotal lobe elevated to form low lamella that extends around lower end of lobe and up on posterior side; front coxa with strong lamella transverse to axis of body, this lamella produced anteriorly to median angle in most males [in *E. (C.) nasicum* (Friese) lateral part of lamella reduced and mesal part extending distad toward coxal spine (male), so that lamella is largely longitudinal]; margin of axilla and scutellum (except for short median section) produced as strong carina or lamella overhanging metanotum and propodeum; scutoscutellar suture nearly closed, similar to scutoaxillar suture (posterior margin of scutum somewhat smooth and shining but not forming broad shiny floor as in forms with an open suture or sulcus) except suture foveate in *E. (C.) nasicum* (Friese); postspiracular fovea of propodeum much larger than spiracle, posterior margin clearly defined but lower end weak or open and upper end open or closed by a carina.

Other features of *Clistanthidium*, mostly in agreement with some or all other subgenera of *Eoanthidium*, include the following: preoccipital ridge noncarinate; subantennal suture strongly arcuate, lower end arising from tentorial pit; hind tibia with sharp line and carina separating inner, keirotrichiate surface from rounded upper surface; propodeum without row of pits across the upper margin except as suggested at the extreme sides; lateral metasomal teeth absent except for tooth at side of T6 and S5 of male, small teeth also at sides of S3 and S4 of male *E. (C.) nasicum*; T7 of male broad; sternal combs of male absent; T7 of male with median point reaching but not extending beyond carinate posterior tergal margin; T6 of female with obtuse or acute lateral angle; between these angles strong, denticulate premarginal ridge without median emargination; tergal margin proper inconspicuous, behind the denticulate ridge, simple except for small median emargination.

Clistanthidium is known from Namibia to Natal Province, South Africa, north to Shaba Province in Zaire and to Tanzania, Mali, Ethiopia, Israel, Iran, Pakistan and Turkey. We have studied *Eoanthidium (Clistanthidium) armaticeps* (Friese), *bituberculatum* (Pasteels), *rothschildi* (Vachal), and *turnericum* (Mavromoustakis) from Africa and *E. (C.) nasicum* (Friese) from Asia.

Etymology: The Latinized form of the Greek *kleistos*, closed, with reference to the closed scutoscutellar suture, plus *Anthidium*.

Genus *Euaspis* Gerstaecker

Euaspis is a paleotropical genus of parasitic bees present in both Africa and Asia. The scutellum of oriental species differs from that of African species in form, being thickened, punctate and hairy in Oriental species rather than thin, lamellate and nearly hairless. On this basis, the Oriental species have been recognized as a separate subgenus, *Parevaspis* Ritsema (Pasteels, 1980). In the absence of other characters, such a separation seems unnecessary. *Parevaspis* is therefore considered to be a junior synonym of *Euaspis*.

Genus *Gnathanthidium* Pasteels

Gnathanthidium is related to *Pseudoanthidium* and should perhaps be regarded as a subgenus of that genus, closest to the subgenus *Micranthidium* as indicated by the strongly carinate, almost lamellate preoccipital ridge, pronotal lobe, omalus, and scutellar truncation; the lack of lateral teeth on T6 and T7 of the male; and the bilobed T7 of the male. It differs, however, in the nearly straight subantennal suture and the not particularly concave S3 to S5 of the male, with no unusual setae except median (not marginal) patches of dense white hairs on S3 and S4, the posterior margins of which are both convex, translucent, and hairless.

Indanthidium new genus

Type species: *Indanthidium ornulatiauda* Michener and Griswold, new species.

In appearance, *Indanthidium* resembles a small (length 6.0-7.5 mm) *Anthidium*, largely because the yellow metaso-

mal bands are divided into four spots each, as in some species of *Anthidium*. Unlike *Anthidium*, the depressed marginal zone of T5 is punctured like the rest of the tergum or a little more densely so in the male, the zone not differentiated and its margin not angulate medially; the posterior margin of T5 and other terga is rather broadly impunctate. *Indanthidium* is similar to *Pseudoanthidium*, with which it agrees in the distinctly arcuate subantennal sutures. It differs from that genus in the unmodified S1 to S6 of the male, without combs or processes and S4 and S5 not especially concave. An unusual feature is T7 of the male which is nearly as broad as T6, with strong median and lateral spines (the latter longest) and with irregular smaller teeth between the median and lateral ones. Another distinctive feature is the maxillary palpus which consists of only one segment.

This genus occurs in India. There is only one known species.

Etymology: India plus *Anthidium*.

Indanthidium crenulaticauda new species

(Figs. 3, 4, 9, 18-21)

MALE: Body length 7.5 mm, forewing length 6.0 mm, head width 3.0 mm. *Head:* Without carinae. Inner orbits converging below. Clypeus flat in profile, upper margin straight except convex laterally, lower lateral margin short, black, with two teeth mesally, lower margin feebly concave, simple, rather thick, not overhanging base of labrum. Labrum impunctate, shining, broadest at base, with strong erect lateral tooth slightly beyond middle. Mandible 3-toothed but upper tooth ending obliquely so that one could recognize four teeth with very shallow emargination between upper two teeth; outer surface coarsely punctate with carinae extending to base. Labial palpus with first segment about half as long as second; maxillary palpus minute, consisting of one almost globular black segment with several bristles. (If this is a second segment, then the first segment is much broader than long and unrecognizable in dry material.) Subantennal sutures distinctly arcuate outward, lines from upper to lower ends parallel, lower ends joining epistomal suture very slightly above tentorial pits. Interantennal distance scarcely larger than antennocular distance; ocelloccipital distance equal to interocellar distance, slightly less than ocellocular distance; genal area narrower than eye seen from side, widest near upper end of eye. Scape not reaching level of anterior edge of anterior ocellus; first flagellar segment almost twice as long as broad, second and third slightly broader than long, following segments slightly longer but tenth only as long as broad, eleventh slightly over 1.5 times as long as broad. *Thorax:* Without carinae except for strong carina, lamellate laterally, on pronotal lobe; omalus rounded; front end of scutum very gradually curved down, without smooth vertical surface; axilla and scutellum with margins rounded seen from above with feeble median scutellar emargination, scarcely overhanging and rounded as seen in profile; scutoscutellar suture almost closed. Propodeum without basal series of pits and postspiracular fovea, profile essentially vertical. Basitarsi about as long as remaining tarsal segments, parallel sided, mid basitarsus as long as tibia; basitarsi with some hairs two to three times as long as widths of basitarsi. Front and mid tibiae each with one small apical spine; hind tibia with apex oblique with median apical angle, tibial spurs nearly straight. Arolia absent. *Metasoma:* T1 with line margining basal concavity except laterally, horizontal surface over half as long as vertical surface; tergal graduli ending near spiracles, not bent back; T6 with weak lateral angle; T7 about three-fourths as broad as T6, short, transverse, with posteriorly directed lateral spine, shorter median spine, and an irregularly spinulose margin between median and lateral spines; S1 to S4 unmodified, S1 to S3 hairy and punctate; S5 with posterior margin broadly concave but without lateral projections; S6 with margin broadly rounded, margin medially with rather dense row of retrorsely curved hairs. Posterior zones of T1 to T6 depressed laterally but scarcely so dorsally, punctation dorsally not different from adjacent parts of terga, posterior impunctate margins about as wide as base of first flagellar segment. *Punctation:* Head and thorax mostly finely and densely punctate, so that surface is dull; punctures of clypeus coarser and on shining surface; scutellum more coarsely punctate and more shining than scutum; propodeum punctate throughout; metasoma with punctures well separated by shining ground, mostly less than a puncture width; T4 to T7 with punctures progressively more irregular and mixed in size and shape; punctures of outer surfaces of tibiae much coarser than those of thorax, hind tibial surface slightly irregular in profile but not tuberculate. *Pubescence:* Moderately long and pallid except short and suberect on dorsum of metasoma and almost absent on S4 to S6; some dusky hairs on frons, vertex, and dorsum of thorax. *Integument:* Black with light yellow markings as follows: basal two-thirds of mandible; clypeus; lower paraocular area, truncately ending at level of antennal socket; lateral transverse stripe on vertex; pronotal lobe; small lateral stripe on anterior margin of scutum; axilla; medially broken posterior stripe on scutellum; anterior and posterior spots on tegula; longitudinal stripe on undersides of fore and mid femora, that on mid femur only on distal half; comparable distal area on hind femur; stripe on outer side of fore tibia; apical and elongate basal spots on outer sides of mid and hind tibiae; outer surfaces of basitarsi; comma-shaped submedian marks on T1 to T5, these coalescing on T6 to form irregular median blotch; transverse lateral marks on T1 to T5; submedian and lateral marks sometimes almost connected posteriorly. Wings dusky, veins black. Small segments of tarsi brown; margins of metasomal terga and sterna brownish; third and following flagellar segments brownish black.

FEMALE: Differs from description of male as follows (in addition to usual sexual characters): Body length 6.0 mm, forewing length 5.2 mm, head width 2.7 mm. *Head:* Clypeus with lower lateral margin lacking teeth, lower margin reflexed forming narrow apical shining ridge, beneath which are five strong denticles. Mandible with five teeth, all separated by acute notches, lowest interspace slightly broader than interspaces 2 to 4 which are equal; teeth 2 to 5 subequal; outer surface of mandible basally with punctures sparse. Interantennal distance slightly less than antennocular distance. Second and third flagellar segments much broader than long, segments four to nine all broader than long. *Thorax:* Hind basitarsus widest near base, tapering slightly toward apex, all basitarsi shorter than tibiae; basitarsal hairs mostly not longer than widths of basitarsi. Front and mid tibial spines strong, acute; apex of hind tibia with strong midapical blunt projection or spine. *Metasoma:* T6 with strong, transverse, preapical, denticulate carina, depressed medially, and separated from apical margin by shiny fovea extending full width of tergum; S6 unmodified; impunctate tergal margins very narrow laterally. *Punctation:* Clypeus coarsely and rather closely punctate on upper half, progressively more finely and densely so on lower half. T4 to T6 with punctures finer than on T1 to T3, less variable in size and shape than in male. *Pubescence:* Scopa white. *Integument:* Basal third of mandible yellow. Clypeus black except for lower lateral areas that nearly meet preapically. Mid tibia with continuous yellow stripe on outer surface; hind tibia with apical yellow area reaching middle of tibia; outer surface of hind basitarsus with distal third black; lateral mark on T5 reduced to transverse streak; T6 black except for four small yellow spots forming a rectangle.

Holotype male, 1 female and 2 male paratypes: INDIA: Poona: Lonavla, January 20, 1959 (F. L. Wain), in the Snow Entomological Museum, University of Kansas, except one male paratype is transferred to the Natural History Museum, London, the other to the USDA Bee Biology and Systematics Laboratory, Utah State University, Logan, Utah.

Etymology: *Crenulatus*, Latin, minutely notched or toothed, plus *cauda*, Latin, tail, with reference to T7 of the male.

Larinostelis new genus

Type species: *Larinostelis scapulata* Michener and Griswold, new species

This is a subgenus of small (6.5 mm long), robust, black bees with extensive yellow markings. Like *Stelis*, the female lacks a scopa. This is the most carinate of all *Stelis*-like bees, with juxtantennal carinae present between the antennal sockets, and with carinae on the pronotal lobe, omalus, axilla, scutellum except median notch, basal zone of propodeum except medially and continuing behind spiracle, dorsal margin of metapleuron, longitudinally on hind basitarsus, transversely on S1 and across base of S6 of the female. The arolia are absent. The axilla is greatly produced laterally, so that it is behind the tegula. The two apical spines of the fore and mid tibiae are minute.

Larinostelis is known from a unique female from Kenya.

It is not clear whether *Larinostelis* is a derivitive of *Stelis* or an independently cleptoparasitic form. In the former case, it would be best regarded as a subgenus of *Stelis*. The discovery of the male should help in deciding this question.

Etymology: *Larinos,* Greek, fat, plus *Stelis,* with reference to the very robust body form.

Larinostelis scapulata new species

(Figs. 22, 23)

FEMALE: Body length 7.0 mm, forewing length 5.5 mm, head width 2.6 mm. *Head:* Without carinae except for high, almost lamellate, juxtantennal carinae that are straight, parallel to one another and separated by less than width of antennal socket. Inner orbits strongly converging below. Clypeus convex in profile, upper margin between subantennal sutures slightly arched, almost as long as upper lateral margin; lower lateral margin less than half as long as any other margin; lower margin straight, denticulate medially. Mandible short, curved, 3-toothed, apices of teeth acute, interspaces equal; outer surface shining, coarsely punctate, carinae strong, not reaching base of mandible. Subantennal sutures nearly straight, longer than diameter of antennal socket, converging downward, joining epistomal suture well above tentorial pits. Interantennal distance much less than antennocular distance; ocelloccipital distance less than interocellar distance which equals ocellocular distance; genal area about half as wide as eye seen from side, widest above middle of eye. Scape not reaching ocelli; first and second flagellar segments subequal in length, much wider than long; following segments progressively longer, seventh and eighth about as long as broad, ninth slightly longer than broad, tenth over 1.5 times as long as broad. *Thorax:* With strong carina on posterior lobe of pronotum and upper half of omalus, with lamella across upper end of metepisternum and across posterior margin of scutellum, the last denticulate; tegula widest at middle; axilla almost square seen from above, extending laterally behind and in contact with tegula (Fig. XXX); scutoscutellar suture foveate, bottom of fovea shiny, fovea divided medially; scutellum strongly produced posteriorly, strongly overhanging metanotum and propodeum, profile acutely angulate, with strong median emargination seen from above. Pronotum with short, slanting, hairless basal area, limited posteriorly by transverse carina, and divided by numerous longitudinal carinae into small, elongate pits, laterally basal zone widening into large fovea delimited by carinae above postspiracular fovea, also delimited by carinae; profile of propodeum behind basal zone vertical. Basitarsi slender, nearly parallel sided, about as long as remaining tarsal segments; hind basitarsus with strong longitudinal carina on outer surface. Apex of hind tibia unmodified. Hind tibial spurs curved near apices, outer one strongly so. Front and middle tibiae each with two short, apical spines, pallid and often difficult to see. Middle tibia nearly as wide as hind tibia, widest near apical third, anterior margin strongly convex, posterior margin straight. Arolia absent. *Metasoma:* T2 widest; T1 with strong line margining basal concavity, horizontal surface somewhat shorter than vertical surface; tergal graduli not bent posteriorly at sides; T6 transverse, not at all pointed apically, not denticulate, with strong, transverse, preapical carina that appears to be the tergal apex when T6 and S6 are closed together; profile of T6 basal to carina short, straight; S6 with strong, transverse basal ridge or carina, surface behind carina with many small tubercles, those near distal tergal margin largest. *Punctation:* Coarse, especially so and cribrate on scutellum, axilla, and mesepisternum; elsewhere punctures mostly separated by about half a puncture width; punctures fine in narrow space between juxtantennal carinae; tergal punctures coarse and rather close laterally, slightly finer and more widely separated middorsally; posterior zones of T1 to T5 slightly depressed, consisting largely of impunctate, translucent marginal bands that are elevated above surfaces of following terga. T6 with surface anterior to carina coarsely, closely, and irregularly roughened. *Pubescence:* Whitish, slightly dusky on dorsum of head and thorax, sparse, short, and inconspicuous, covering surface only on paraocular area; hairs rather dense on fore and mid basitarsi where largest hairs are slightly longer than width of basitarsus. *Integument:* Head and thorax black, metasoma red brown, except the following bright yellow: clypeus; lower paraocular area; small spot on vertex laterally; pronotal lobe in part; anterior spot on tegula; transverse mark laterally along anterior margin of scutum; axilla; narrow subapical, medially-interrupted band on scutellum; large triangular mark on mesepisternum below pronotal lobe; ventral surfaces of fore and mid femora; tibiae except ventral surfaces; fore and mid basitarsi; large lateral spot on T1, on T2 slightly larger, T3 with complete band; T4 to T6 yellow. The following red brown: mandible, scape, first two flagellar segments, tegula posteriorly, legs and terga except as marked with yellow, and S1 to S6. Flagellar segments three to ten dusky brown. Wings dusky, veins black.

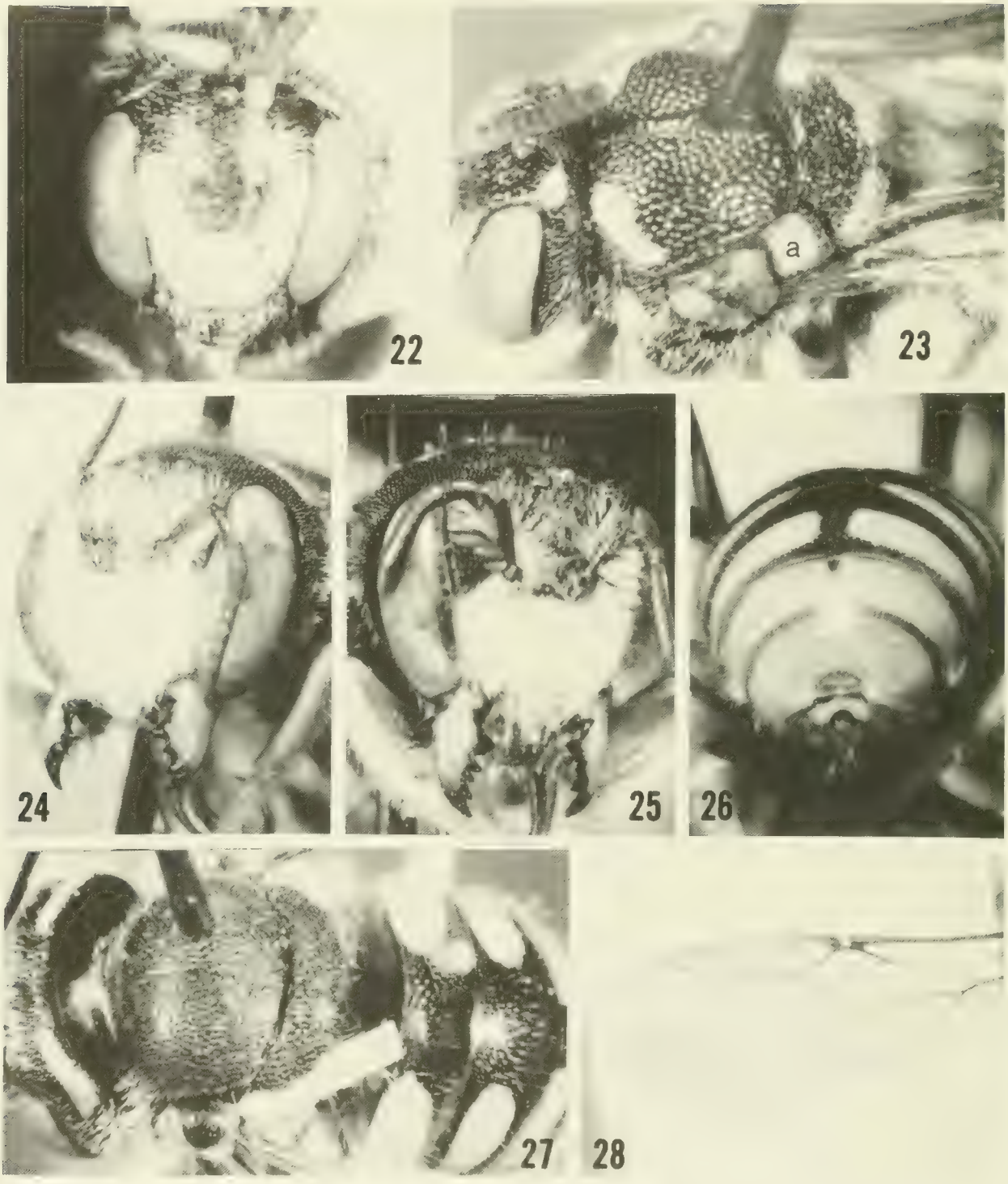
Holotype female: KENYA: 26 miles (42 km) southwest of Nairobi, 5300 feet (1631 m), 11 January 1970, M. E. Irwin and E. S. Ross, in the California Academy of Sciences, San Francisco.

Etymology: *Scapulata,* Latin, with shoulder blades, referring to the unusual lateral positions of the axillae.

Genus *Pachyanthidium* Friese

Key to the Subgenera of *Pachyanthidium*

1. Eyes hairless; preoccipital carina absent laterally, behind eyes 2
—Eyes with abundant, short hairs; preoccipital carina present laterally, behind eyes (mandible of female 4-toothed) 3
2. Arolia present; mandible of female 4-toothed (Namibia) ..... *Ausanthidium*
—Arolia absent; mandible of female usually 5- to 10-toothed or denticulate, 4-toothed only in *P. (P.) micheneri* Pasteels (Africa) ..... *Pachyanthidium* s. str.
3. T3 to T5 each with slender lateral spine; ocelli small, diameter about equal to width of base of first flagellar segment; hind coxa not carinate; arolia present in male, absent in female (Africa, southern Asia) ..... *Trichanthidium*
—T3 to T5 without lateral spines; ocelli of ordinary size, diameter greater than width of base of first fla-



Figs. 22, 23. *Larmostelis scapulata* Michener and Griswold, female. **22.** Face. **23.** Dorsolateral view of head and thorax to show axilla (a) behind tegula.

Figs. 24-28. *Pseudoanthidium (Tuberanthidium) bracheatum* Michener and Griswold. **24.** Laterofrontal view of male face showing mandibular dentition. **25.** Same for female. **26.** Apex of male metasoma. **27.** Dorsum of female with slip of paper under edge of axilla and side of scutellum to show outline. **28.** Forewing of female.

gellar segment; hind coxa carinate; arolia absent (possibly with very minute arolia in both sexes) (east Africa, Arabian Peninsula) ..... *Trichanthidiodes*

Subgenus *Ausanthidium* Pasteels

There is a single species, *Pachyanthidium (Ausanthidium) ausense* (Mavromoustakis), new combination.

This subgenus has not hitherto been placed in *Pachyanthidium,* but nearly all its characters support such a placement. A small fovea behind the propodeal spiracle, reported by Pasteels (1969a), that might support the original placement in *Anthidiellum,* is ill defined, no wider than the spiracle itself, and probably merely the edge of the spiracular area, not a fovea in the sense of that of *Anthidiellum* and other genera.

Subgenus *Pachyanthidium* Friese s. str.

A remarkable feature of the subgenus is the variability in dentition of the female mandibles, from 4-toothed to multitoothed and to minutely serrate. Males also are variable in mandibular dentition, from 4-toothed to 8-toothed. In spite of this variation, the species are similar in most of their characters and constitute a morphologically rather homogeneous taxon.

Trichanthidiodes new subgenus

Type species: *Pachyanthidium semiluteum* Pasteels, 1984.

Presumably because of its hairy eyes, *P. semiluteum* was placed in *Trichanthidium* by Pasteels (1984). It differs, however, in many ways including its extensive yellow coloration. The following are subgeneric characters; in those marked (1) *Trichanthidiodes* agrees with *Pachyanthidium* s. str., in those marked (2) it agrees with *Ausanthidium;* and in those marked (3) it agrees with *Trichanthidium.*

Eyes hairy (3); ocelli not reduced in size (1, 2); mandible of female 4-toothed (2, 3); omalar carina continued directly across ventral midline (3); wings not strongly darkened (2); arolia absent in male (1); arolia absent in female (1, 3); hind coxa carinate ; T1 with transverse carina not double laterally, i.e., without preapical carina (1, 2); terga with wide, transparent, impunctate margins (1, 2); terga without lateral spines, with rounded lateral swellings (1, 2); S4 of male without comb (1, 2); S5 of male with comb (1); gonostylus of male with club delimited basally by strong carina (3); T6 of female with small, deep midapical emargination (1, 2); S5 of female flat, not biconvex or bilobed (1, 2).

This subgenus is known from Kenya and Saudi Arabia. There is one species, *P. (Trichanthidiodes) semiluteum* Pasteels.

Etymology: *Trichanthidium* plus the Greek suffix -odes, similar to or resembling.

Genus *Plesianthidium* Cameron

Plesianthidium consists of four subgenera that agree in the lack of pale markings except on the face of the male and in other characters indicated in the key to genera and below. The subgenera are different enough from one another, however, that they have frequently been given generic status. Common features, other than those indicated in the key to genera, are (1) lack of carinae except sometimes on the pronotal lobe and sometimes on the preoccipital ridge behind the vertex, (2) the straight subantennal sutures arising at or near the tentorial pits, (3) rounded scutellum not or little overhanging the metanotum, in profile rounded or in the subgenus *Spinanthidiellum,* angled, (4) presence of arolia, (5) the tendency of T6 of the male to be trifid or trilobed (not in the subgenus *Spinanthidiellum),* (6) the small, but little-exserted male T7 which is 3-toothed or in the subgenera *Plesianthidium* s. str. and *Carinanthidium* with the middle tooth reduced to a minor convexity between two long, widely separated teeth, (7) male sterna little modified except S5 with apical comb, absent in the subgenus *Spinanthidium,* and S6 characteristically lobed or with various convexities, (8) male gonostyli simple, slightly expanded and hairy apically, with two small teeth at apex in *Plesianthidium* s. str. Of the four subgenera, two, *Plesianthidium* and *Spinanthidium,* are closely related and might well be united.

Key to the Subgenera of *Plesianthidium*

1. Preoccipital ridge with carina behind vertex; T6 of male truncate, without lateral tooth, distally with longitudinal ridge, highest at posterior margin of tergum; mandible less than twice as long as broad (Cape Province) ..... *Spinanthidiellum*
—Preoccipital ridge not carinate; T6 of male with median truncate or rounded to pointed projection, rarely weakly produced, and strong lateral tooth; mandible over twice as long as broad 2
2. S6 of female with strong longitudinal median carina; hind trochanter of male with mesal subapical spine; pubescence almost all black except white on face of male (South Africa) ..... *Carinanthidium*
—S6 of female not carinate; hind trochanter of male not spined; pubescence brown to gray, or whitish on face and venter 3
3. T7 of male strongly trifid, median tooth or lobe exceeding lateral ones; S5 of male without apical comb; maxillary palpus 2-segmented (Cape Province) ..... *Spinanthidium*
—T7 of male with median tooth reduced to low prominence so that tergum is essentially bifid; S5 of male with apical comb; maxillary palpus 3-segmented (Cape Province) ..... *Plesianthidium* s. str.

Genus *Pseudoanthidium* Friese

Pseudoanthidium is here used in a broad sense to include numerous species having compact bodies, commonly with the form of *Anthidium* s. str.; except in the subgenus *Micranthidium* the head is thick and the tibiae are tuberculate on the outer surfaces. Even in *Micranthidium* the tibiae are coarsely punctate.

Key to the Subgenera of *Pseudoanthidium*

1. Gena margined posteriorly by distinct preoccipital carina (gena narrower than eye seen from side) 2
—Gena without preoccipital carina (scutellum rounded or medially emarginate seen from above; tibiae tuberculate on outer surfaces at least in female; male without lamellate lateral lobe on S3; clypeus of female with discal hairs straight) 3
2. Preoccipital carina behind vertex strongly produced back over front of thorax as a lamella; posterior basitarsus of male more than twice as long as broad (scutellum broadly truncate in dorsal view, posterior margin angulate laterally near axilla; tibiae not tuberculate but coarsely punctate; lateral lobe of S3 of male lamellate; clypeus of female with discal hairs bent down (Africa, Arabian Peninsula) ..... *Micranthidium*
—Preoccipital ridge behind vertex rather weakly carinate; posterior basitarsus of male less than twice as long as broad (west Africa) ..... *Semicarinella*
3. Propodeum shagreened; T6 of male with strong apical flange which is medially emarginate; fore and mid basitarsi of female with long plumose hair (Tanzania and southern Africa) ..... *Tuberanthidium*
—Propodeum shiny where not punctate; T6 of male without emarginate flange; fore and mid basitarsi of female with long hair not plumose 4
4. T6 of female with surface broadly and conspicuously excavated; T5 of female with small, midapical marginal projecting lobe; exposed part of T7 of male longer than exposed part of T6, very deeply bilobed; S5 of male without strong lateral tooth or lobe (Mediterranean basin to central Asia and Sudan) ..... *Exanthidium*
—T6 of female with surface largely convex; T5 of female without midapical lobe; exposed part of T7 of male shorter than exposed part of T6, weakly to strongly bilobed; S5 of male with strong lateral process 5
5. Clypeal apex of female fully exposed, coarsely denticulate, protruding; S3 and S4 of male broadly emarginate or S3 with median V-shaped emarginarion and S5 with apicolateral projection, all without combs or specialized hairs (Palearctic) ..... *Royanthidium*
—Clypeal apex of female largely hidden by hair, without shining, protruding premarginal ridge; S3 of male with comb of long, wavy bristles and S5 with comb at apex of apicolateral projection ..... *Pseudoanthidium* s. str.

Subgenus *Pseudoanthidium* Friese s. str.

The synonymy of *Pseudoanthidium* and *Paranthidiellum* indicated in the List of Genus-Group Names above is based in part on identification of *Anthidium alpinum* Morawitz, the type species of *Pseudoanthidium*. We have seen specimens of various species identified as *alpinum*. One of them agrees with the original description, having a black clypeus in the male, an unusual feature, and we believe it is true *alpinum*. All of them, however, agree in subgeneric characters with *Paranthidiellum* which we therefore place as a synonym of *Pseudoanthidium* s. str. Pasteels (1969a) and Warncke (1980), however, place *Anthidium barbatum* Mocsary and *serraticeps* Friese in the synonymy of *A. alpinum*. This cannot be correct, for the type of *serraticeps* in Berlin is a larger, robust species of the subgenus *Royanthidium;* it is a female with a bare, projecting dentate clypeal margin. Morawitz said that *A. alpinum* (based on one male) is a species with the aspect of *Pseudoanthidium lituratum* (Panzer), which is a *Pseudoanthidium* s. str. as here understood. As to *Carinellum,* it contains only two species and its distinctive characters, which appear to be apomorphic relative to other *Pseudoanthidium,* do not seem to warrant a separate subgenus.

Subgenus *Royanthidium* Pasteels

As indicated in the above list, we consider *Reanthidium* Pasteels to be a synonym of *Royanthidium*. *Reanthidium* differs from *Royanthidium* in having the preoccipital ridge carinate behind the vertex. We judge that a separate subgeneric name is not needed for the one species with this carina. *P. (R.) nigricolle* (Morawitz), placed in *Reanthidium* by Pasteels, is a synonym of *P. (R.) melanurum* (Klug), the type species of *Royanthidium,* according to Warncke (1980).

Subgenus *Semicarinella* Pasteels

Semicarinella is based on a single male specimen that we have not seen. It may be merely a species of *Micranthidium* with unusual characters.

Subgenus *Tuberanthidium* Pasteels

Pasteels considered that an unusual feature of the males of *Tuberanthidium* was the 5-toothed mandible. Most specimens have four teeth; often the number of teeth on opposing mandibles differs; in one specimen one mandible has only three teeth. The definition of this subgenus has been considerably modified to include the following new species.

Pseudoanthidium (Tuberanthidium) brachiatum new species

(Figs. 5, 6, 24-28)

This species differs in several major characters from other species of *Tuberanthidium;* our initial view was that it should be placed in a new subgenus. However, we decided that another monotypic subgenus is unnecessary and have broadened the definition of *Tuberanthidium* instead. It differs from other species of *Tuberanthidium* in the more angulate (but not carinate) omalus, lack of a dorsal bulge on the mandible of the female, gently convex apical margin of S3 of the male with wavy bristles (on midapical part of sternum) inconspicuous and shorter than white hairs located more

laterally, and black combs on apical part of apicolateral projection of S5 of the male and pair of small combs on the margin of S5 on either side of the midline. The structure of S5 is similar to that of various other subgenera of *Pseudoanthidium* and reinforces our view that *Tuberanthidium* should be included in *Pseudoanthidium*.

MALE: Body length 8.0 to 10.0 mm; forewing length 7.2 to 8.0 mm; head width 3.8 to 4.2 mm. *Head:* Without carinae. Inner orbits converging below. Clypeus flat in profile, upper margin strongly arched; lower lateral margin very short, lower margin straight, apparently slightly undulate, completely covered by long, white, downward directed, plumose hair; clypeus not overhanging base of labrum. Labrum widest at base, otherwise parallel sided, with longitudinal depression between midlateral ridges. Mandible 4-toothed, apices of teeth acute; interspaces equal and acute notches; lower and upper teeth larger than two median teeth; outer surface of mandible largely smooth, shining, sparsely punctate, without carinae. Second segment of labial palpus over 1.5 times length of first; maxillary palpus short, 2-segmented. Subantennal sutures strongly arcuate outward, lines from upper to lower ends parallel, lower ends joining epistomal suture much above tentorial pits. Interantennal distance over 1.5 times antennocular distance; ocelloccipital distance greater than ocellocular distance, which is greater than interocellar distance; genal area nearly as wide as eye seen from side, widest behind upper third of eye. Scape not reaching level of anterior margin of anterior ocellus, first flagellar segment 1.5 times as long as wide, second wider than long, subsequent segments progressively longer, tenth about as long as broad and eleventh over 1.5 times as long as broad. *Thorax:* Without carinae except one on pronotal lobe; upper half of omalus strongly angular but not carinate; scutum with anterior end curved strongly down but without vertical surface; axilla and scutellum transverse, margins rounded as seen from above with weak median emargination, posterior edges acute as seen in profile, overhanging metanotum and propodeum; scutoscutellar suture narrowly foveate, posterior edge of scutum impunctate, supplementing width of fovea. Propodeum without basal series of pits and postspiracular fovea. Front femur thick at base, forming ventral angle at base. Basitarsi as long as remaining tarsal segments together, parallel sided, all shorter than tibiae, front and mid basitarsi with some hairs about twice as long as basitarsal diameter. Front and middle tibiae each with one small, blunt apical spine; hind tibia with apex oblique with median apical convexity; tibial spurs slightly curved at apices. Arolia absent. *Metasoma:* T1 and T2 widest; line margining concavity of T1 distinct, extending to side of tergum, horizontal surface of T1 over half as long as vertical surface; graduli of T1 to T4 ending near spiracles, on T5 curving posteriorly and forming strong carina reaching posterior tergal margin and forming small lateral lobe or very blunt tooth; T6 without lateral tooth, with projecting apical lamella that is absent in middle third, leaving depressed emargination flanked by highest part of apical lamella; T7 small, exposed part one-third as wide as T6, bilobed with semicircular emargination between lobes; S1 to S3 simple with abundant long hair; S3 with yellowish wavy bristles arising near margin of middle third, these bristles inconspicuous, their curvature not strong, hairs lateral to them white and longer than wavy bristles; S4 with margin broadly and distinctly concave; S5 margin also concave, with very small black comb on each side of midline, produced at side to long, slender, lateral arm directed posteromesally, each with apical black comb of six or seven teeth; S6 with broad median, apically notched projection. Posterior zones of T1 to T5 only slightly depressed medially, distinctly so laterally, more finely punctate than rest of terga, nearly half of each zone forming broad impunctate margin elevated above base of following tergum. *Punctation:* Rather dense, finer on frons and vertex than on thorax, clypeus shining with punctures of upper part well separated and shallow, lower margin of supraclypeal area impunctate, shining; mesepisternum with punctures contiguous; propodeum strongly shagreened, with punctures only on basal and lateral areas; outer surfaces of tibiae coarsely punctate and moderately tuberculate; metasomal punctures well separated by shining ground. *Pubescence:* Sparse except long, plumose, dense, and white on apical clypeal margin, thoracic venter, and S1 to S3; pubescence of vertex, dorsum of thorax, and metasomal terga dusky except yellowish posteriorly on metasoma; otherwise pubescence white or on side of thorax and on legs, yellowish. *Integument:* Black with yellow markings as follows: mandible except black teeth and apical and inner margins; clypeus; lower supraclypeal area to about level of antennal sockets; lower paraocular area up to same level, slightly higher next to socket; transverse mark laterally on vertex; spot on front of tegula; legs except coxae, trochanters, and femora basally; broad transverse bands on T1 to T5, broadly interrupted on T1, progressively less so on succeeding terga to incompletely or not so on T5; T6, T7, and sterna entirely yellow. Posterior margins of T1 to T6 translucent brown grading to translucent yellow on posterior terga. Wings dusky, veins black.

FEMALE: Differs from description of male as follows (in addition to usual sexual characters): Body length 8.5 to 9.0 mm; forewing length 7.0 mm; head width 3.9 mm. *Head:* Lower margin of clypeus with three denticles, hidden as in male. Mandible 5-toothed, upper tooth largest, obliquely truncate, thus suggestive of additional tooth (Fig. 25). Interantennal distance little greater than antennocular distance; ocelloccipital distance equal to or less than ocellocular distance, which is greater than interocellar distance. All flagellar segments except first and last (which are about as in male) broader than long. *Thorax:* Fore femur not angulate at base. Hind basitarsus widest near base, tapering; long hairs of basitarsi plumose. Apical spines of tibiae sharp, large on fore and mid tibiae. *Metasoma:* Lateral longitudinal carina of T5 as in male. T6 with profile flat except for strongly elevated apical lamella across area about half as wide as basal (exposed) width of tergum, the lamella produced apically to form projection on each side of small median notch; laterally, near end of lamella, it forms small shoulder nearer median notch than lateral extremity of T6. S6 unmodified. *Punctation:* Clypeus less shining, coarsely and closely punctate except for uppermost margin which is smooth, like lower margin of supraclypeal area. Outer surfaces of tibiae more strongly tuberculate than in males. Middorsal parts of T1 to T4 with punctures mostly separated by several puncture widths. *Pubescence:* Scopa yellowish white. Hairs of coxae, trochanters, and bases of femora hooked or somewhat wavy. *Integument:* Supraclypeal area yellow only along lower margin, extending up toward antennal base laterally; small segments of tarsi yellowish brown; yellow band of T5 narrowly interrupted; parts of femora and metasomal sterna yellow brown.

Holotype male, 1 male and 2 female paratypes: TANZANIA: Tarangiri National Park, 2300 feet (708 m) altitude, 23 January 1970 (M. E. Irwin and E. S. Ross). The holotype and female paratypes are in the California Academy of Sciences, San Francisco; the male paratype, in the USDA Bee Biology and Systematics Laboratory, Utah State University, Logan, Utah.

Etymology: *Brachiatus,* Latinized Greek meaning with arms, referring to the armlike lateral processes of S5 of the male.

Genus *Rhodanthidium* Isensee

Key to the Subgenera of *Rhodanthidium*

1. T6 of male with median, produced truncation or rounded process and lateral tooth or strong shoulder; S5 of male with strong lateral tooth and median marginal comb; omalus weakly carinate above; margin of scutellum with sharp edge laterally; female with apical projection of fore and mid tibiae narrowly bidentate (western Palearctic) . . . . *Rhodanthidium* s. str.
—T6 of male simple or with scarcely produced broad truncation, with or without strong shoulder or weak lateral tooth; S5 of male without lateral tooth, without comb; omalus not carinate or weakly so above

in *R. (Asianthidium) caturigense* (Giraud) and its relatives; margin of scutellum rounded, not forming sharp edge except in *R. (Asianthidium) caturigense;* female with apical projection of fore and mid tibiae either not notched or widely and shallowly emarginate 2

2. Trifid apex (median tooth sometimes broad and rounded or truncate) of T7 of male occupying full width of tergum; pronotal lobe with lamella or carina, weak in *R. (Asianthidium) glasunovi* (Morawitz); head with background color black (Mediterranean basin to central Asia) . . . . . *.Asianthidium*

—Trifid apex of T7 of male much narrower than tergum, which has lateral angles so that tergum is 5-toothed; pronotal lobe without or with very weak carina; head largely yellow (Turkey to central Asia) . . . . . *.Meganthidium*

Subgenus *Asianthidium* Popov

The synonymy indicated in the list above is based on similarity and the small number of species involved. *Asianthidium* in its original narrow sense, *Axillanthidium,* and *Oxyanthidium* each contains only a single species. *Asianthidium* in the sense of *R. (A.) glasunovi* (Morawitz) seems the most deserving of separate subgeneric recognition if the subgenus as here understood is to be divided. Its weak rather than strong carina on the pronotal lobe and the elevated median process of T7 of the male (suggesting *Rhodanthidium* s. str.) differentiate it from other species. *R. (A.) aculeatum* (Klug), the species placed in *Oxyanthidium,* differs from other species in the strongly denticulate and laterally angulate margin of T6 of the female and the translucent preapical lamella above the apex of S6 of the female, so that the sternum has a double margin.

Placement of *Axillanthidium* in the synonymy of *Asianthidium* is based on Warncke (1980), who considered *Axillanthidium axillare* Pasteels as a synonym of "*Anthidium caturigense ducale* Morawitz" and on a specimen of *caturigense,* the type species of *Trianthidium,* with axillae emarginate and anteriorly angulate, nearly as accentuated as in Pasteels' illustration of *axillare.* Other specimens of *caturigense* have the emargination and anterior angle scarcely evident.

Subgenus *Rhodanthidium* Isensee s. str.

Most of the species form a unified group, but *R. (R.) infuscatum* (Erichson) is quite distinctive and has been given the genus name *Bellanthidium* Pasteels. Since there is only one such species and its relationship to the others is clear, a subgenus for it seems unnecessary.

Genus *Stelis* Panzer

The suggestion has been made that the subgenus *Protostelis* might be derived from *Trachusa,* and that *Stelis* therefore might be polyphyletic. *Protostelis* resembles *Trachusa* in its robust body, well-developed vertex, broad middle tibia, and the often oblique vein cu-v of the hind wing with the second abscissa of M+Cu shorter than in other *Stelis* although not as short as in most *Trachusa.* However, *Protostelis* does not have the reflexed male T7 characteristic of *Trachusa* and does have *Stelis*-like features such as the two spines on the apices of the front and middle tibiae and apically expanded, angulate male gonostyli. We therefore regard *Protostelis* as a subgenus of *Stelis,* not related to *Trachusa,* but either the *Stelis*-like or the *Trachusa*-like characters might result from convergence.

Key to Old World Subgenera of *Stelis*

1. Clypeus produced well over mandibles and apex bilobed, strongly so in female; anterior spine of front and middle tibiae conspicuous, enlarged, curved posteriorly (Palearctic, to Kenya) . . . . . *.Stelidomorpha*

—Clypeus not greatly produced over mandibles, truncate or subtruncate; anterior spine of front and middle tibiae less than twice the size of posterior spine 2

2. Axilla projecting laterally beyond lateral margin of scutum; scutellum strongly projecting over metanotum and propodeum (southeast Asia) . . *.Malanthidium*

—Axilla not projecting laterally beyond margin of scutum; scutellum at most weakly projecting over metanotum and propodeum 3

3. Scutellum not carinate laterally; head and thorax without light markings; hind tibial apex with two spines or angles, one near outer middle of apical tibial margin (if with only one spine, *S. simillima* Morawitz, not on posterior apical angle) or the spines united to form truncate margin, the area sparsely hairy so that structure is easily seen; omalus not carinate (Holarctic, Oriental) . . . . . *.Stelis* s. str.

—Scutellum carinate laterally; head and thorax with light markings; hind tibial apex with a single spine (sometimes a mere angle) largely hidden in hairs near the posterior apical angle of the tibia, in front of which the apex of the tibia is a convex margin; omalus usually carinate 4

4. Hind basitarsus with carina along inner dorsal angle; mid tibia flattened, apically enlarged, twice as wide apically as basally; S1 with transverse carina overhanging apical margin (Holarctic) . . . . . *.Protostelis*

—Hind basitarsus without carina; mid tibia not flattened, little enlarged apically, apex at most 1.5 times basal width; S1 without transverse carina (Palearctic) . . . . . *.Pseudostelis*

Subgenus *Malanthidium* Pasteels

Anthidium malaccense Friese, the type species of *Malanthidium* and known only from the male, was marked "*?Stelis*" in the original description; its transfer to *Stelis* is therefore not entirely surprising. We have seen a female of a related

species that lacks a scopa and is obviously a *Stelis* s. l. Pasteels (1969a) described *Stelis malaccensis* (Friese) (as *Malanthidium)* (new combination) in some detail. His figure 138 shows a midapical clypeal denticle, also mentioned in his description. No such denticle is present on the type (and only known?) specimen although there is a small shiny place on the clypeal margin.

Subgenus *Protostelis* Friese

The placement of *Doxanthidium* in the synonymy of *Protostelis* in the above List of Genus-Group Names is based on descriptions and figures (see Pasteels, 1969a), on Warncke (1992) and on a personal communication from G. van der Zanden (1993). Friese (1911) also suggested that *Anthidium paradoxum* Mocsary might be a *Protostelis* and Warncke (1980) placed it in *Stelis.*

Two groups, one composed of larger species, the other of smaller, have commonly been included in *Protostelis.* Pasteels (1969a) indicated that the larger and smaller groups might be independent and thus separate subgenera. We place the larger species in the subgenus *Protostelis* and the smaller ones in the subgenus *Pseudostelis.* The size differences are not consistent, but in general apply; *S. signata* (Latreille) is often only 5 mm long, *S. strandi* is 6 to 8 mm long, while the larger species measure 10 mm or more. Both groups differ from other *Stelis* in the 3-segmented maxillary palpi and the combination of scutellum carinate laterally but not strongly overhanging the propodeum. Both have light markings on the head and thorax and the omalus frequently carinate. The anterior surface of the mesepisternum is always concave. *Protostelis* differs from *Pseudostelis* and other *Stelis* in several ways. In *Protostelis* the apical angle of the hind tibia is dorsal rather than along the outer face; the hind basitarsus has a longitudinal carina along the inner dorsal margin; the mid tibia is flattened, much enlarged apically and in the female is clothed with dense decumbent hair; and the apical width of the female mandible is 1.5 to 2.0 times the narrowest width. *Protostelis* is further distinguished from *Pseudostelis* by the long vertex, wide impunctate apical tergal bands, and the strongly carinate preapical margin of S1.

Genus *Trachusa* Panzer

Several characters that are often stable within a genus vary in *Trachusa.* Arolia are commonly present but sometimes greatly reduced or absent. Combs on S4 and S5 of the male are sometimes present but also often absent, and may vary even within a species (of the subgenus *Heteranthidium,* see Brooks and Griswold, 1988). The number of mandibular teeth of the female is commonly four but may be three as in *Trachusa* s. str. or five, six or seven, as in the subgenera *Massanthidium* and *Congotrachusa.* The number of segments in the maxillary palpus may be four or reduced to three.

Key to the Old World Subgenera of *Trachusa*

1. Mandible of female with three more or less equidistant teeth; maxillary palpus as long as maximum width of galea, 4-segmented (yellow markings absent except for face of male) (western Palearctic) ..... *Trachusa* s. str.
—Mandible of female 4- to 7-toothed; maxillary palpus shorter than width of galea, 3- or 4-segmented 2
2. Second recurrent vein entering second submarginal cell basal to second transverse cubital vein; T7 of male with median basal projection (Mediterranean basin to central Asia) ..... *Archianthidium*
—Second recurrent vein meeting or distal to second transverse cubital vein; T7 of male without basal projection 3
3. Subantennal suture distinctly arcuate outward; gonoforceps of male deeply bifid, Y-shaped (male unknown in *Orthanthidium*) (Palearctic) 4
—Subantennal suture nearly straight; gonoforceps of male not Y-shaped (not palearctic) 5
4. Scutellum truncate posteriorly as seen from above, margin curved sharply forward laterally to meet longitudinal margin of axilla; eyes of female conspicuously diverging below; interocellar distance of female much less than half ocelloccipital distance (southeast China, Taiwan) ..... *Orthanthidium*
—Scutellum broadly rounded except medially emarginate; lateral margin of axilla convex but in general slanting; eyes of female subparallel; interocellar distance about half of ocelloccipital distance (Mediterranean basin to southeast China, Oriental) ..... *Paraanthidium*
5. Omalus distinctly carinate, carina extending onto ventral surface of thorax close to middle coxa (Africa) ..... *Massanthidium*
—Omalus not carinate 6
6. Arolia present in female, absent in male; S4 and S5 of male without combs (southeast Asia) ..... *Metatrachusa*
—Arolia minute if present; S4 and S5 of male with combs as in Paraanthidium (west Africa) *Congotrachusa*

Subgenus *Archianthidium* Mavromoustakis

Although this subgenus was not included in *Trachusa* by Pasteels (1969a), we believe that it easily falls within that genus. Superficially, because of its size (12.5-18.0 mm long), form, and abundant yellow markings, it resembles the North American subgenus *Heteranthidium* and well-marked species of *Paraanthidium,* although unlike the former, the yellow metasomal bands at least on T1 are broken medially. It is indeed similar to and probably related to *Heteranthidium,* as indicated especially by the large, volsellalike process from the apex of the male gonocoxite (genitalia of three species illustrated by Mavromoustakis, 1939). All of its characters

fall within the range of variation for *Heteranthidium* except the broken metasomal bands, the position of the second recurrent vein (see key to subgenera), and the midbasal, retrorse, blunt or truncate process of T7 of the male. (T7 does not have two slender apical processes as suggested by Pasteels, 1969a, fig. 12. Instead there are two strong carinae on a high ridge extending from the basal process toward the apex of the tergum.) Arolia are present in both sexes and the female mandible often does not show four recognizable teeth, the upper two being united in a sometimes undulate margin.

Subgenus *Paraanthidium* Friese

Megachile steloides Bingham, 1896, the type species of *Protanthidium,* a junior synonym of *Paraanthidium,* when transferred to *Anthidium,* became a junior secondary homonym of *Anthidium steloides* Spinola, 1851. It was therefore renamed as *Anthidium longicorne* by Friese, 1902. Even though the two species are no longer in the same genus, Friese's name is retained, as *Trachusa longicornis* (Friese), according to Article 59(b) of the International Code of Zoological Nomenclature.

Orthanthidium, known only from females, could be considered as a synonym of *Paraanthidium.* If the unknown male of *Orthanthidium* has the characteristic features of *Paraanthidium,* the two subgenera should be united.

Trachusoides new genus

Type species: *Trachusoides simplex* Michener and Griswold, new species.

This genus contains a large species (length 12 mm) similar in form to *Apianthidium* and *Trachusa.* The head of the female is black, the thorax has limited pale yellow markings, and the metasoma is yellowish red. A unique character is the simple female claws, breaking down an otherwise constant character of cleft or toothed claws in female Anthidiini. (The inner tooth is very small, however, in *Serapista.*) Except for a strong carina on the pronotal lobe, there are no carinae on the head and thorax. Basal or postspiracular pits or foveae on the propodeum are absent. The middle tibia (female) is narrower than the hind tibia, with anterior and posterior margins equally and symmetrically convex seen laterally, the apex as narrow as the base of the tibia; these tibial characters differentiate it from both *Trachusa* and *Apianthidium.* The male is unknown.

Trachusoides is found in southern India and known from a single specimen of *T. simplex* Michener and Griswold.

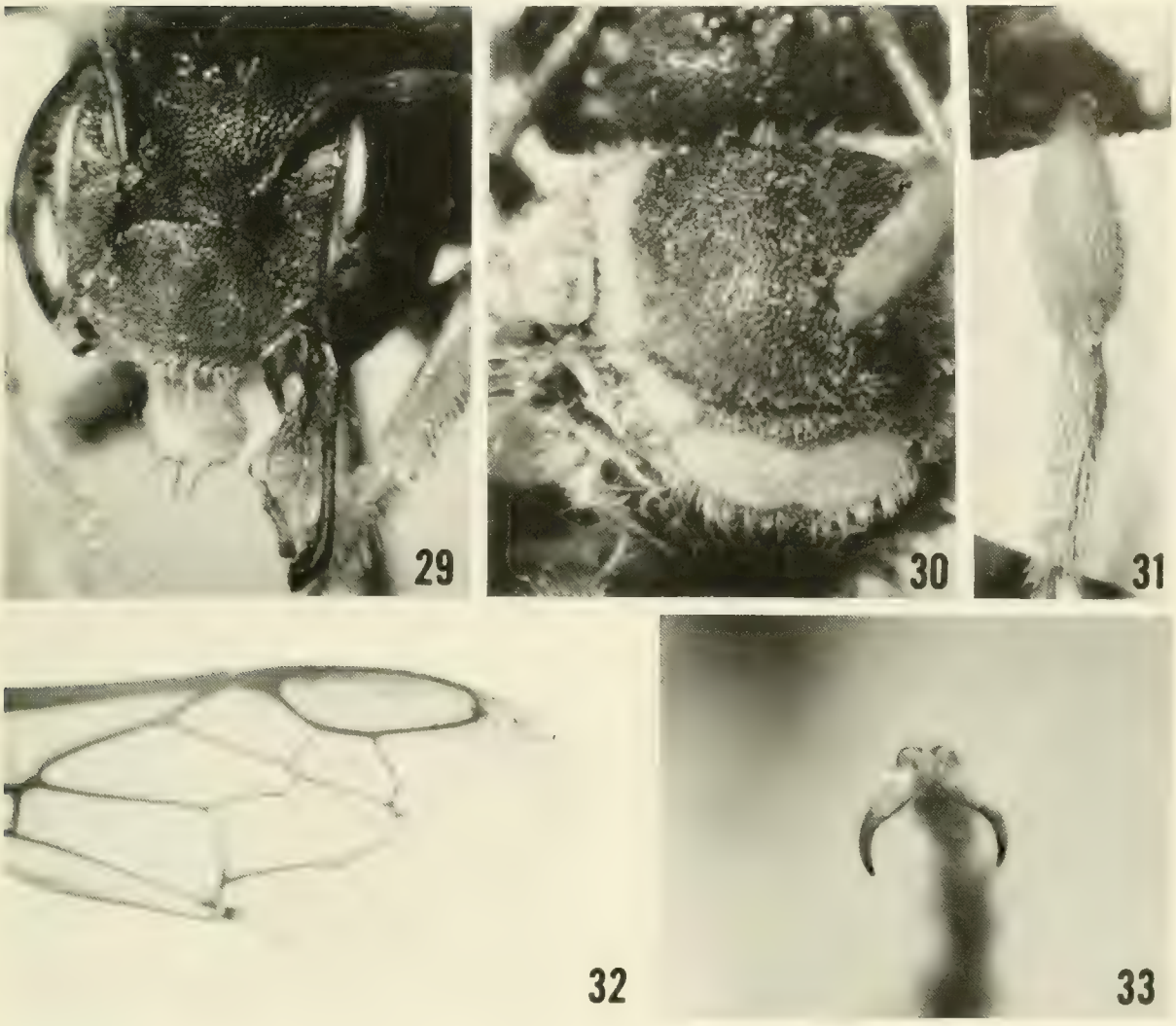
The only known specimen of *Trachusoides* is described rather fully below. It is similar in many features to *Apianthidium.* When the male is known, it may prove to be a species of that genus in spite of the simple claws of the female, which are unique among Anthidiini.

Etymology: *Trachusa* plus "-oides," similar to.

Trachusoides simplex new species
(Figs. 29-33)

Structural characters that differ from those of *Apianthidium* are italicized.

FEMALE: Body length 12.0 mm, forewing length 8.0 mm, head width 3.9 mm. *Head:* Carinae absent. Inner orbits subparallel, upper halves gently concave. Clypeus convex in profile, hexagonal, upper margin between subantennal sutures arched, lower margin with eight denticles (lateral ones weak) between which arise tufts of bristles (median ones longest). Labrum rather weakly sclerotized, little longer than broad, broadest at base and at apical fourth, surface minutely punctate, apex with tufts of erect bristles (Fig. 29). Mandible rather long, 4-toothed (Fig. 29), outer surface dull and minutely roughened except for smoother distal margin and apex of rutellum, outer and condylar ridges very narrow but strongly elevated, shining, outer ridge extending from cap of rutellum about halfway to base of mandible, condylar ridge extending somewhat farther. First segment of labial palpus about twice as long as second; maxillary palpus small, 3-segmented, second segment much longer than first, third minute. Subantennal sutures straight, *longer than diameter of antennal socket,* converging downward, joining epistomal suture above tentorial pits. Interantennal distance about twice antennocular distance; head well developed behind and above ocelli so that *ocelloccipital distance is nearly twice interocellar distance; ocellocular distance about 1.5 times interocellar distance;* ocelli largely below upper ocular tangent; *genal area about as wide as eye seen from side, widest near middle of eye.* Scape reaching about level of middle of anterior ocellus; first flagellar segment 1.5 times as long as broad, second and third broader than long, fourth nearly as long as broad, *following segments progressively longer until ninth is about 1.5 times as long as broad;* tenth over twice as long as broad. *Thorax:* Without carinae except for *strong carina on pronotal lobe;* omalus rounded; front end of scutum gradually bent downward, without smooth vertical surface; axilla and scutellum with posterior margins convex seen from above except for small median scutellar emargination, these margins not carinate, rounded in profile, strongly overhanging metanotum and base of propodeum; scutoscutellar suture closed, not forming fovea. Propodeum with no indication of basal pits or postspiracular fovea, profile convex, upper two-fifths being declivous but not vertical, curving gradually onto vertical lower three-fifths. Basitarsi each longer than remaining tarsal segments together, widest near bases and slightly tapering; mid basitarsus as long as tibia; hind basitarsus over three times as long as broad. Front and mid tibiae each with single, strong, blunt, mid-apical spine largely hidden by short pale hair; *for shape of mid tibia see generic diagnosis;* hind tibia with apex truncate, apical margin only slightly convex medially; *tibial apurs nearly straight. Claws simple.* Arolia absent. *Metasoma:* T1 to T3 widest; T1 with carina margining basal concavity, horizontal surface less than half as long as vertical surface; tergal graduli ending near spiracles, not bent posteriorly; T6 unmodified, profile straight, margin not denticulate; S6 slightly exceeding T6 medially, not modified. Posterior zones of terga scarcely depressed; no conspicuous impunctate margins. *Punctation:* Dense throughout, finer on clypeus and lower paraocular and genal areas than rest of head and thorax; propodeum punctate throughout; tibiae more coarsely punctate than body but surfaces not tuberculate; posterior depressed zones of T1 to T5 and all of T6 more finely punctate than clypeus; sterna with basal and apical zones not or sparsely punctate. *Pubescence:* Pallid but somewhat yellowish on head and thorax, dusky on upper part of head, more orange on metasoma and legs; scopa orange. Hairs of clypeus mostly erect and very short, scattered longer hairs preapically; bristles of clypeal and labral apices orange; lower margin of mandible with series of about six widely spaced long, erect bristles (as in *Apianthidium*). Rest of head and thorax with hairs rather sparse, longest on sides and venter of thorax and on propodeum. Metasoma with hairs short and suberect dorsally, quite dense, denser and directed posteriorly on posterior tergal



Figs. 29-33. *Trachusoides simplex* Michener and Griswold, female. **29.** Slightly lateral view of face to show mandibular dentition. **30.** Slightly lateral view of thoracic dorsum. **31.** Middle tibia and basitarsus, outer view. **32.** Forewing. **33.** Claws of middle leg.

zones and T6. Scopa long and dense, including that on S6. *Integument:* Black on head and thorax except dull pallid yellow on broad lateral margin of scutum, almost whole axilla, and posterior two-thirds of scutellum. Second and third flagellar segments, part of pronotal lobe and preaxilla orange brown. Tegula, tarsi, tibiae, and apices of femora orange. Wings strongly dusky brown, darker near costal margins, veins and stigma black. Metasoma orange, bases of T1 to T5 more yellowish, fading to deeper orange in posterior zones.

Holotype female: INDIA: Karnataka State: Appangala, January to June, 1978 (O. P. Dubey). We are indebted to Dr. B. Mallik of the University of Agricultural Sciences, Bangalore, India, for making available the specimen of *T. simplex;* it is deposited at his request in the National Pusa Collection, Division of Entomology, Indian Agricultural Research Institute, New Delhi. Dr. Mallik has provided further details about the collecting site. The specimen was actually collected on 1 June 1978. Appangala is a small village about 40 km from Mercara in the Coorg district of Karnataka, 75°40'22"E, 12°32'35"N, altitude about 1100 m; rainfall about 2500 mm annually; vegetation wet deciduous.

Etymology: *Simplex,* Latin, simple, with reference to the simple claws.

LITERATURE CITED

Bingham, C. T. 1898. On some new species of Indian Hymenoptera. Journal of the Bombay Natural History Society 12: 115-130, pl. A.

Cameron, P. 1902. Descriptions of new genera and species of Hymenoptera collected by Major C. G. Nurse at Deesa, Simla and Ferozepore, Part II. Journal of the Bombay Natural History Society 14: 419-449.

Cameron, P. 1905. On the Hymenoptera of the Albany Museum, Grahamstown, South Africa. Records of the Albany Museum 1: 185-265.

Cockerell, T. D. A. 1904a. The genus *Apista,* etc. Canadian Entomologist 36: 357.

Cockerell, T. D. A. 1904b. The bees of southern California.—1. Bulletin of the Southern California Academy of Sciences 3: 3-6.

Cockerell, T. D. A. 1930. African bees of the family Megachilidae (Anthidiinae, *Serapista* and *Lithurgus*) mainly from Liberia and the Belgian Congo. Revue de Zoologie et de Botanique Africaines 19: 43-55.

Cockerell, T. D. A. 1931. Heriadine and related bees from Liberia and the Belgian Congo. Revue de Zoologie et de Botanique Africaines 20: 331-341.

Cockerell, T. D. A., and W. P. Cockerell. 1901. Contributions from the New Mexico Biological Station.—IX. On certain genera of bees. Annals and Magazine of Natural History (7)7: 46-50.

Fabricius, J. C. 1804. Systema Piezatorum. iii-xiv + 15-349 + 1-30 pp. Braunschewig.

Fairmaire, L. 1858. Ordre Hymenopteres, pp. 263-267, figures on pl. 10, *in* J. Thomson, Voyage au Gabon, Histoire Naturelle des Insectes et des Arachnides, Archives Entomologiques, vol. 2.

Friese, H. 1895. Die Bienen Europa's, Theil I, pp. 1-128. Berlin: Friedländer.

Friese, H. 1898. Die Bienen Europa's, Theil IV, pp. 1-303, 1 pl. Innsbruck: C. Lampe.

Friese, H. 1902. Zwei neue Bienengattungen (Hym.). Zeitschrift für Systematische Hymenopterologie und Dipterologie 2: 186-187.

Friese, H. 1905. Die Wollbienen Afrikas. Genus *Anthidium*. Zeitschrift für Systematische Hymenopterologie und Dipterologie 5: 65-75.

Friese, H. 1908. 5. Apidae, pp. 119-168. *In* Y. Sjostedt, Wissenschaftliche Ergebnisse der schwedischen zoologischen Expedition nach dem Kilimanjaro, dem Meru und den umgebenden Massaisteppen Deutsch-Ostafrikas 1905-1906, Band 2, Abt. 8 (Hymenoptera), Pt. 5 (Apidae). Stockholm: Palmquist.

Friese, H. 1911. Apidae I, Megachilinae. Das Tierreich, Lieferung 28: xxvi + 440 pp. Berlin: Friedländer.

Friese, H. 1923. Die europäischen Bienen. Berlin and Leipzig: Gruyter. xvii + 456 pp., 33 pl.

Gerstaecker, A. 1857. [Bees and wasps collected in Mozambique]. Monatsberichte, Akademie der Wissenschaften, Berlin, vom 29, October 1857, pp. 460-464.

Gistel, J. N. F. X. 1848. Naturgeschichte des Thierreichs, für Höhere Schulen. xvi + 216 pp., 32 pls. Stuttgart: Hoffmann.

Isensee, R. 1927. A study of the male genitalia of certain anthidiine bees. Annals of the Carnegie Museum 17: 371-382, pl. xxxii.

Klug, F. 1807. Vergleichung der Gattungen der Hautflügler, Piezata Fabr. Hymenoptera Linn. Jur. Magazin fur Insektenkunde 6: 189-198.

Krombein, K. V. 1951. Additional notes on the bees of the Solomon Islands. Proceedings of the Hawaiian Entomological Society 14: 277-295.

Lepeletier de Saint-Fargeau, A. L. M. 1841. Histoire Naturelle des Insectes—Hyménoptères, vol. 2, pp. 1-680.

Mavromoustakis, G. A. 1939. New and little-known bees of the subfamily Anthidiinae (Apoidea).—Part I. Annals and Magazine of Natural History (11)3: 88-97.

Mavromoustakis, G. A. 1951. Further contributions to our knowledge of the Ethiopian Anthidiinae (Hymenoptera: Apoidea) and their classification. Annals and Magazine of Natural History (12)4: 962-981.

Mavromoustakis, G. A. 1953. New and little-known bees of the subfamily Anthidiinae (Apoidea).—Part VI. Annals and Magazine of Natural History (12)6: 834-840.

Mavromoustakis, G. A. 1958. Bees (Hymenoptera, Apoidea) of Attica (Greece), Part I. Annals and Magazine of Natural History (13)1: 433-447.

Mavromoustakis, G. A. 1963a. On the bees (Hymenoptera, Apoidea) of Lebanon, Part III. Annals and Magazine of Natural History (13)5: 647-655.

Mavromoustakis, G. A. 1963b. Further contributions to our knowledge of the Ethiopian Anthidiinae (Hymenoptera: Apoidea) and their classification.—Part 2. Annals and Magazine of Natural History (13)6: 481-499.

Michener, C. D. 1948. The generic classification of the anthidiine bees. American Museum Novitates 1381: 1-29.

Michener, C. D. In press. Some genus-group names of bees. Journal of the Kansas Entomological Society.

Morawitz, F. 1875. Mellifera Latr., pp. 1-160. *In* A. P. Fedtschenko, Reisen in Turkestan, Zoogeographische Folge, Teil V, pt. I, Apidae Genuinae. Moscow.

Noskiewicz, J. 1961. Beiträge zur Kenntnis der paläarktischen Arten der Gattung *Stelis*. Polskie Pismo Entomologiczne 31: 113-133.

Panzer, G. W. F. 1804. Faunae Insectorum Germanicae. Heft 86.

Panzer, G. W. F. 1806. Kritische Revision der Insektenfauna Deutschlands, [14] + 271 pp., 2 pls. Nürnberg.

Pasteels, J. J. 1968. Statut, affinités et origines des Anthidiinae parasites. Naturaliste Canadien 95: 1055-1063.

Pasteels, J. J. 1969a. La systématique générique et subgénérique des Anthidiinae (Hymenoptera, Apoidea, Megachilidae) de l'ancien monde. Mémoires de la Société Royale d'Entomologie de Belgique 31: 1-148.

Pasteels, J. J. 1969b. New Anthidiinae (Hymenoptera, Apoidea, Megachilidae) from the Mediterranean area and from the Near East. Israel Journal of Entomology 4: 409-434.

Pasteels, J. J. 1972. Révision des Anthidiinae (Hymenoptera Apoidea) de la région indo-malaise. Bulletin et Annales de la Société Royale Belge d'Entomologie 108: 72-128.

Pasteels, J. J. 1980. Révision du genre *Euaspis* Gerstaecker. Bulletin et Annales de la Société Royale Belge d'Entomologie 116: 73-89.

Pasteels, J. J. 1984. Révision des Anthidiinae (Hymenoptera, Apoidea, Megachilidae) de l'Afrique subsaharienne. Mémoires de la Classe des Sciences, Académie Royale de Belgique (2)19(1): 1-165.

Popov, V. B. 1941. Notes on *Dianthidium sibericum* (Eversm.) and a new species of *Stelis* Panz. Entomologisk Tidskrift 62: 222-224.

Popov, V. B. 1950. Generic groupings of the mid-Asian bee subfamily Anthidiinae. Doklady Akademii Nauk SSSR 70: 315-318 [in Russian].

Popov, V. B. 1956. New and little-known bees from central Asia. Entomologicheskoe Obozrenie 35: 159-171 [in Russian].

Radoszkowski, O. 1874. Supplément indispensable à l'article publié par W. Gerstaecker in 1869, sur quelques genres d'Hyménoptères. Bulletin de la Société Imperiale des Naturalistes de Moscou 48(1): 132-164.

Ritsema, C. 1874. [*Zodion*, Hymenoptera, etc.]. Tijdschrift voor Entomologie 17: lxviii-lxxv.

Roig-Alsina, A., and C. D. Michener. 1993. Studies of the phylogeny and classification of long-tongued bees. University of Kansas Science Bulletin 55: 124-162.

Romankova, T. G. 1988. A new far-eastern bee of the tribe Anthidiini. Vestnik Zoologii 1988(4): 25-30.

Smith, F. 1854. Catalogue of the Hymenopterous Insects in the Collection of the British Museum, Part 2: 198-465, pls. vii-xii.

Spinola, M. 1808. Insectorum Liguriae Species Novae aut Rariores. Vol. 2, ii + 262 pp. Genuae: Gravier.

Timberlake, P. H. 1941. Ten new species of *Stelis* from California. Journal of the New York Entomological Society 49: 123-137.

Tkalců, B. 1967. Bemerkungen zur Taxonomie einiger palaärktischer Arten der Familie Megachilidae. Acta Entomologica Bohemoslovaca 64: 91-104.

Urban, D. 1992. *Gnathanthidium*, gen. n. de Anthidiinae da América do Sul. Revista Brasileira de Zoologia 9: 337-343.

Warncke, K. 1980. Die Bienengattung *Anthidium* Fabricius, 1804 in der Westpaläarktis und in turkestanischen Becken. Entomofauna 1: 119-209.

Warncke, K. 1992. Die westpalaärktischen Arten der Bienengattung *Stelis* Panzer, 1806. Entomofauna 13: 341-376.

ANNOUNCEMENT

The *University of Kansas Science Bulletin* (continuation of the *Kansas University Quarterly*) is an outlet for scholarly scientific investigations carried out at the University of Kansas or by University faculty and students. Since its inception, volumes of the *Bulletin* have been variously issued as single bound volumes, as two or three multi-paper parts or as series of individual papers. Issuance is at irregular intervals, with each volume prior to volume 50 approximately 1000 pages in length. Effective with volume 50, page size has been enlarged, reducing the length of each volume to about 750 pages.

The supply of all volumes of the *Kansas University Quarterly* is now exhausted. However, most volumes of the *University of Kansas Science Bulletin* are still available and are offered, in exchange for similar publications, to learned societies, colleges and universities and other institutions, or may be purchased at $30.00 per volume. Where some of these volumes were issued in parts, individual parts are priced at the rate of 3 cents per page. Current policy, initiated with volume 46, is to issue individual papers as published. Such separata may be purchased individually at the rate of 7 cents per page, with a minimum charge of $1.50 per separate. Subscriptions for forthcoming volumes may be entered at the rate of $30.00 per volume. All communications regarding exchanges, sales and subscriptions should be addressed to the EXCHANGE LIBRARIAN, UNIVERSITY OF KANSAS LIBRARIES, LAWRENCE, KANSAS 66045.

Reprints of individual papers for personal use by investigators are available for most recent and many older issues of the *Bulletin*. Such requests should be directed to the author.

The International Standard Serial Number of this publication is US ISSN 0022-8850.

Editor
Charles D. Michener

Editorial Board
Meredith Lane, *Chairman*
James S. Ashe
George W. Byers
Christopher Haufler
Norman A. Slade

THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. 55, No. 10, pp. 329-376 September 20, 1995

OCT 13 1995

HARVARD
UNIVERSITY

Amphibians and Reptiles from Northern Departamento Loreto, Peru: Taxonomy and Biogeography

William E. Duellman and Joseph R. Mendelson III[1]

TABLE OF CONTENTS

Abstract 329
Resumen 330
Introduction 330
Acknowledgments 330
Materials and Methods 331
Species Accounts 335
Plate 1 340
Biogeography 364
Literature Cited 373

ABSTRACT

Collections of amphibians and reptiles from the vicinities of San Jacinto and Teniente López in the northern part of Departamento Loreto in Amazonian Peru include 68 species of amphibians and 46 of reptiles. Among five new species are two *Eleutherodactylus*, one *Adelophryne*, one *Phyllomedusa*, and one microhylid not assigned to a recognized genus. *Hyla cabrerai* Cochran and Goin, 1970, and *Osteocephalus planiceps* Cope, 1874, are resurrected from the synonymies of *Osteocephalus buckleyi* and *Osteocephalus taurinus*, respectively. *Hyla albopunctulata* and *Phyllomedusa coelestis* are redescribed. *Hyla albopunctulata, Osteocephalus cabrerai, Eleutherodactylus quaquaversus, Adelophryne adiastola*, and *Lepidoblepharus hoogmoedi* are reported for the first time from Peru, and a notable northern range extension is reported for *Hyla koechlini*. Comparisons of three sites show considerable difference in species composition and reflect patchiness of the rainforest. Comparisons of composition, abundance, diel activity, microhabitat, and masses of anurans and lizards from two study zones also reveals considerable differences. The taxonomic composition of the anurans and lizards at the sites in northern Loreto is more like that at Santa Cecilia, Ecuador, than those at Cocha Cashu and Cuzco Amazónico, Peru.

Key words: Amphibia, Reptilia, Amazonian Peru, taxonomy, new species, biogeography.

[1] Division of Herpetology, Natural History Museum, and Department of Systematics and Ecology, The University of Kansas, Lawrence, Kansas 66045-2454, USA

RESUMEN

Coleciones de anfibios y repiles efectuados en los alrededores del San Jacinto y Teniente López en la parte norte del Departamento de Loreto en la región amazónica del Perú incluye 68 especies de anfibios y 46 especies de reptiles. Entre cinco especies nuevas están dos especies de *Eleutherodactylus*, una *Adelophryne*, una *Phyllomedusa*, y un microhílido no asignado a un género reconocido. *Hyla cabrerai* Cochran y Goin, 1970, y *Osteocephalus planiceps* Cope, 1874, se resucitan de las sinonimias de *Osteocephalus buckleyi* y *Osteocephalus taurinus*, respectivamente. *Hyla albopunctulata* y *Phyllomedusa coelestis* se describen nuevamente. *Hyla albopunctulata, Osteocephalus cabrerai, Eleutherodactylus quaquaversus, Adelophryne adiastola,* y *Lepidoblepharus hoogmoedi* se registran para primera vez del Perú, y se amplía notablemente al norte el Earea de distribución de *Hyla koechlini* hacia al norte. Las comparaciones de la composición, abundancia, actividad diaria, microhábitat, y biomass de los anuros y los saurios de las dos zonas de estudio también revelan diferencias considerables. La composición taxonómica en anuros y saurios de los localidades del norte de Loreto es más similar a la de Santa Cecilia, Ecuador, que a las de Cocha Cashu y Cuzco Amazónico, Perú.

PALABRAS CLAVES: Amphibia, Reptilia, Región Amazónica del Peru, taxonomía, especies nuevas, biogeografía.

INTRODUCTION

The last two decades have witnessed numerous studies on the herpetofauna of the Amazon Basin. Major faunal studies embrace anurans and lizards near Belém, Brazil (Crump, 1971), the herpetofauna of Santa Cecilia, Ecuador (Duellman, 1978), anurans at Panguana, Peru (Toft and Duellman, 1979; Schlüter, 1984); the reptiles in the Iquitos region, Peru (Dixon and Soini, 1986); the lizards at Cuzco Amazónico, Peru (Duellman, 1987), the herpetofauna at Cocha Cashu, Peru (Rodríguez and Cadle, 1990); the herpetofauna at the INPA Reserves near Manaus, Brazil (Zimmerman and Rodrigues, 1990), lizards at Balbina, Brazil (Martins, 1991); the herpetofauna at Cuzco Amazónico, Peru (Duellman and Salas, 1991); the anurans at Cocha Cashu, Peru (Rodríguez, 1992); snakes from a site in Rondônia, Brazil (Silva, 1993), and lizards of Amazonian Brazil (Avila-Pires, 1995). Comparisons of herpetofaunal communities were provided by Duellman (1989, 1990). Neotropical anuran diversity was summarized by Duellman (1988), and anuran biogeography of cis-Andean tropical lowlands was analyzed by Heyer (1988).

Despite this seemingly intense effort, our knowledge of the Amazonian herpetofauna is far from complete. It is becoming increasingly obvious that the Amazon rainforest is highly heterogeneous (Gentry, 1988) and that environmental diversity is reflected in patterns of diversity and distribution among the animals inhabiting the rainforest. Consequently, visits to previously unstudied areas invariably result in the documentation of significant range extensions and the discovery of new species. Likewise, previously unknown species commonly are found in areas that have been studied previously. As an example of the rate of discovery, 18% of the 256 species of amphibians in the Amazon Basin have been named since 1980.

This report is based on collections of amphibians and reptiles made as part of a biological survey at two previously unstudied localities in extreme northern Departamento Loreto, Peru. The localities are within an oil concession currently being operated by Occidental Peruana Inc. (formerly Occidental Petroleum Company) in the region disputed by Ecuador and Peru but controlled as a *zona militar* by Peru since 1941. In 1974 the Occidental Petroleum Company of Peru began exploration in a concession (Block-1AB); this operation was expanded and now consists of many camps connected by roads to the major facility at Andoas (Fig. 1). Our purpose herein is to provide: (1) accounts of the 114 species of amphibians and reptiles found at sites in northern Loreto, Peru, (2) compare the samples from these sites, and (3) compare the herpetofauna of this region with those at other regions in the central and upper Amazon Basin.

ACKNOWLEDGMENTS

The field studies in northern Peru were made possible by the generous support of Occidental Peruana Inc. We are greatly indebted to Carlos Delius, President; Joaquin Rodríguez, Vice President for Operations; and especially Clark Hull, Environmental Manager. Work in Block-1AB was facilitated by José Luis Adrianzen, René La Rosa, Robert Palmer, Joseph Pine, Charles Schwab, and Aubry C. Sudduth. Our collections benefited from material found by our coworkers in the field—César Ascorra, Constantino Aucca, Richard A. Leschen, Romel Mora de Aguila, Alfonso Miranda, Richard O. Prum, Robert M. Timm, David M. Webb, and Neal Woodman. We are grateful to Robin Foster for botanical data, to Diane M. Debinski and Paul Rich for physical environmental data, and to Gilberto Pezo for installing traps and drift fences and maintaining trails. Field work was supported in part by a grant (DEB 9311799) from the National Science Foundation (W. E. Duellman, Principal Investigator) and the Neotropical Biological Diversity Fund of the Natural History Museum, University of Kansas. Arrangements with Occidental Peruana Inc. and for Peruvian permits were handled by the Asociación de Ecología y Conservación (ECCO); we are grateful to B. Anthony Luscombe, President of ECCO, for his efforts in our behalf. Permits were issued by Ing. Absalón Vásquez Villanueva, Ministerio de Agricultura. For the loan of specimens or provision of working space in their respective institutions, we are grateful to Alice G. C. Grandison (British Museum), Marinus S. Hoogmoed (Rijksmuseum van Natuurlijke Historie), Edmond Malnate (Academy of Natural Sciences of Philadelphia), Roy W. McDiarmid (National Museum of Natural History), and Teresa Cristina Sauer de Avila-Pires (Museu Paraense

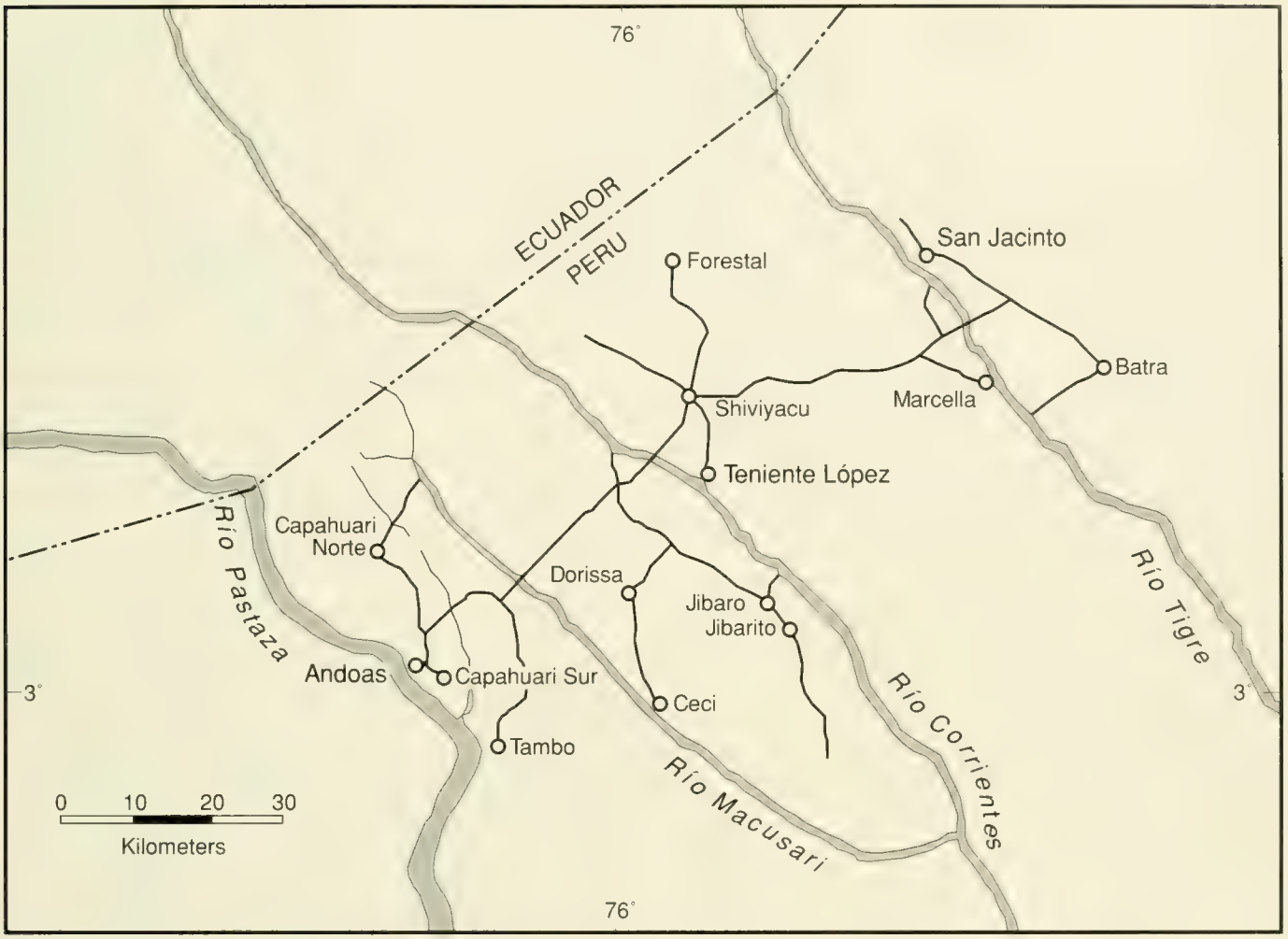


Fig. 1. Map of northern Departamento Loreto, Peru, showing major rivers and localities mentioned in text.

Emilio Goeldi). We thank David A. Kizirian for assistance with the identification of gymnopthalmid lizards, William W. Lamar for permission to include some data recorded by him, Amy Lathrop for faithfully executing drawings of specimens, John E. Simmons for his skillful work in the darkroom, Linda Trueb for aid with the graphics, James Diffendorfer and Erik R. Wild for assistance with some of the statistical analyses, William W. Lamar and John D. Lynch for constructive comments on the manuscript, and Ignacio de la Riva for assistance with the Resumen. All photographs were taken by William E. Duellman; cost of the color plate was funded by the Herpetology Research Fund, Natural History Museum, The University of Kansas.

MATERIALS AND METHODS

A pilot project to assess the biodiversity at sites in Block-1AB in the northern part of Departamento Loreto, Peru, was planned and approved in December 1992. The project was a cooperative effort by the Center of Neotropical Biological Diversity of the Natural History Museum at The University of Kansas, the Asociación de Ecología y Conservación of Lima, Peru, and Occidental Peruana Inc.

In January 1993 study sites were selected by William E. Duellman and Martín Timaná, and together with Tómas Luna C. they surveyed the study zones and laid out 25 20 X 20 meter quadrats distributed throughout each study zone so as to incorporate the diversity of habitats. Thus, at San Jacinto quadrats were placed along the border of a black-water swamp and in secondary and primary forest. At Teniente López quadrats were placed along small streams, on slopes, and on ridge tops in primary forest. In April 1993 physical environmental data were collected by Diane M. Debinski and Paul M. Rich; during the same time Tómas Luna C. surveyed elevations of the quadrats. Geographic coordinates were determined by means of a Garmin GPS 75 Personal Navigator™ in July 1993 by William E. Duellman.

The location and description of each of the places from which specimens were obtained are (Figs. 2 and 3):

San Jacinto Camp.—02°18'42.8"S, 75°51'57.9"W, 180 m (south helipad). Large clearing with grass; many buildings, concrete sidewalks, and dirt roads.

San Jacinto Study Zone.—02°18'44.8"S, 75°51'46.0"W, 180 m (entrance of trail from road). Partially disturbed rainforest on low rolling terrain with a system of 25 20 X 20 m quadrats in an area extending from the west edge of a blackwater lagoon (175 m elevation) for 280 m to the northeast and 160 m to the northwest and encompassing elevations of 175–190 m.

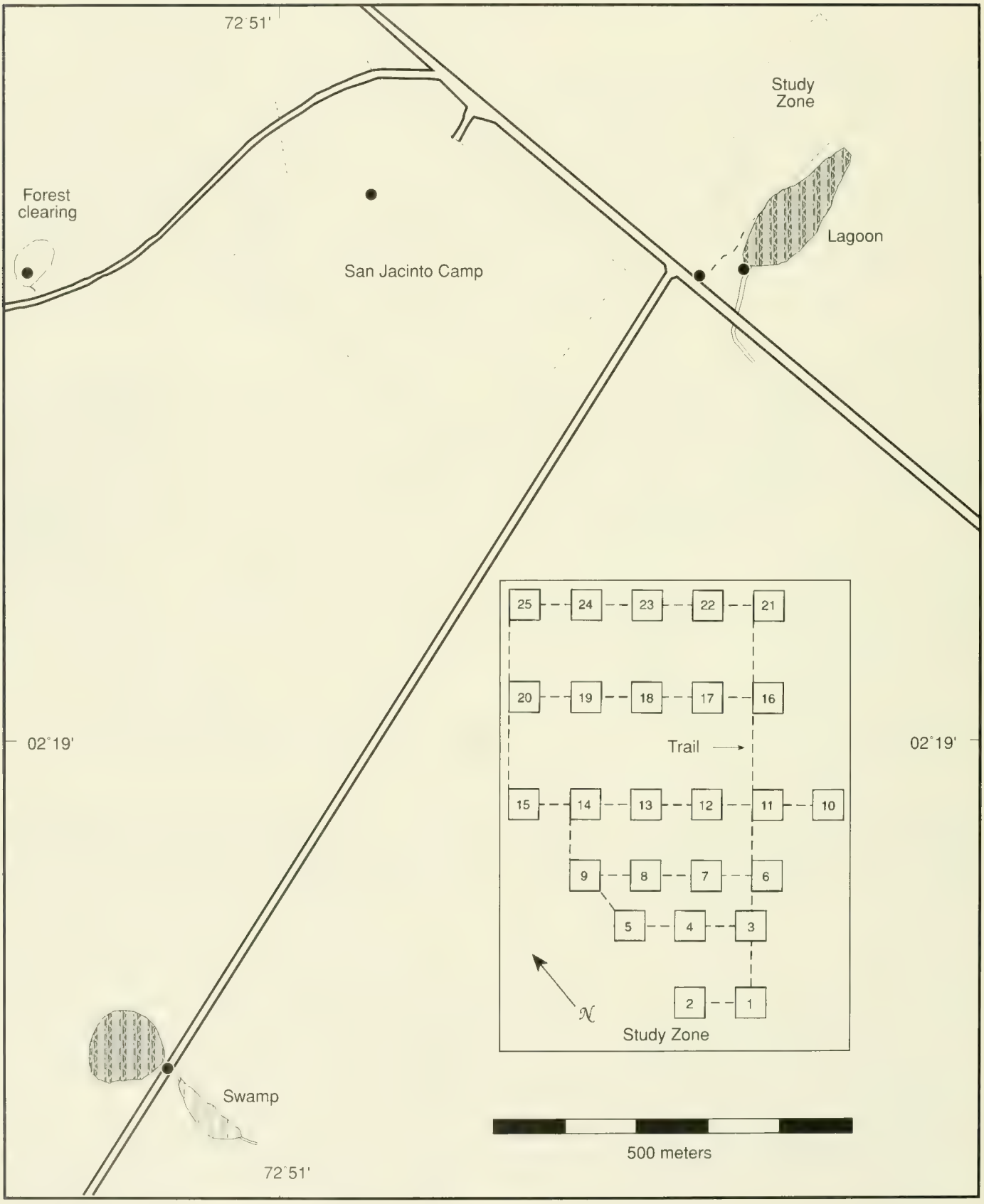


Fig. 2. Map of the San Jacinto area showing roads and sites mentioned in the text. The study zone is shown in detail in the inset. Dots are sites of readings with a geographic positioning device.

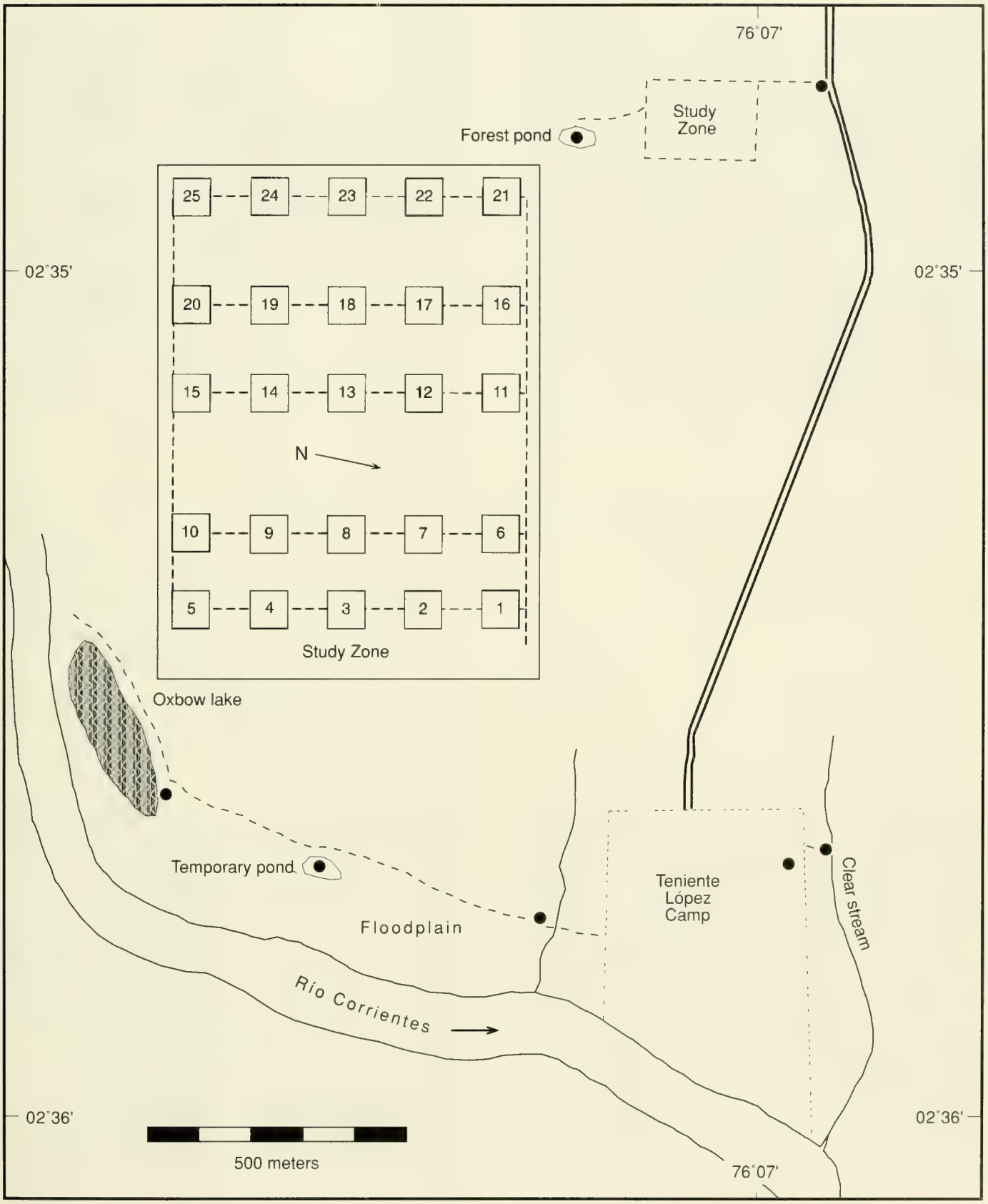


Fig. 3. Map of the Teniente López area showing roads and sites mentioned in the text. The study zone is shown in detail in the inset. Dots are sites of readings with a geographic positioning device.

Fig. 4. Lagoon at San Jacinto. Quadrats 1, 3, and 6 in the study zone are at the border of the lagoon on the left. July 1993.

Fig. 5. Swamp to the east of the road just south of the San Jacinto Camp. July 1993.

San Jacinto Lagoon.—02°18'44.2"S, 75°51'44.8" W, 175 m (south edge). A black-water lagoon (approximately 150 X 40 m) to the north of the road at Km 47.1, bordered on the south by marshy clearing and elsewhere by rainforest (Fig. 4).

San Jacinto Swamp.—02°19'11.0"S, 75°52'03.3", 175 m (at culvert). A site about 0.5 km south of the San Jacinto Camp on the road to Well Sites 16, 17, and 20. The road dams a large pond (approximately 80 m diameter) to the west and a grassy swamp to the east; both are surrounded by relatively undisturbed rainforest (Fig. 5).

San Jacinto Forest Clearing.—02°18'45.0"S, 75°52'08.2", 180 m (in center). A newly cleared (May 1993) area within rainforest (approximately 120 X 80 m) to the north of the road west of San Jacinto Camp.

Teniente López Camp.—02°35'40.4"S, 76°06'56.8"W, 200 m (parking lot in front of staff dining hall). Large, cleared ridge top with many buildings, grass, and dirt roads.

Teniente López Stream.—02°35'40.0"S, 76°06'55.0"W, 190 m (pump house). A swift, clear tributary of the Río Corrientes, 3–5 m wide with sandy bottom completely shaded by partially disturbed rainforest.

Teniente López Floodplain.—02°35'44.8"S, 76°07'15.0"W, 185 m (east edge). Disturbed rainforest on floodplain of Río Corrientes west of the Teniente López Camp.

Teniente López Temporary Pond.—02°35'40.8"S, 76°07'30.3", 185 m (middle). An irregular water-filled depression (approximately 70 X 20 m) in disturbed rainforest on the floodplain west of Teniente López.

Teniente López Oxbow Lake.—02°35'38.3"S, 76°07'41.7"W, 185 m (southeast shore). An oxbow of the Río Corrientes in the floodplain west of the Teniente López Camp (Fig. 6).

1.5 km N Teniente López Forest Pond.—02°34'52.5"S,

Fig. 6. Oxbow lake on floodplain of the Río Corrientes west of the Teniente López Camp. July 1993.

Fig. 7. Forest pond to the west of the study zone 1.5 km N Teniente López. July 1993.

76°07'12.6"W, 310 m (middle). A permanent or semipermanent pond supporting *Heliconia* in a depression in rainforest to the west of the study zone (Fig. 7).

1.5 km N Teniente López Study Zone.—02°18'43.2"S, 75°51'58.1"W, 333 m (trail at road 1.5 km N Teniente López). Study zone of a system of 25 quadrats 20 X 20 m extends west from 118 to 365 m from the road along a trail at a bearing of 288° and south for a distance of 180 m. Rolling terrain (310–340 m) with steep slopes and small, sandy bottomed streams in primary rainforest.

Throughout the text, San Jacinto is abbreviated SJ, Teniente López TL, and 1.5 km north of Teniente López NTL.

One soil sample was collected at the center point of each quadrat in both study zones using an auger 8.75 cm in diameter; the auger was turned into the soil to a depth of 15 cm, and samples were sealed in plastic bags. Samples were analyzed at Soil, Plant, and Water Testing Laboratory, Colorado State University, Ft. Collins, Colorado. Soil samples were analyzed for calcium, magnesium, sodium, potassium, percent organic matter, Total Olsen phosphate, total organic carbon, nitrogen, carbon/nitrogen ratio, pH, chlorine, and cation exchange capacity. Hydrometer readings were used to estimate the percentage of sand, silt, and clay. Texture was noted as sandy clay loam, clay loam, sandy loam, clay, or combination thereof.

All trees ≥ 10 cm in diameter at breast height (DBH) in the 25 quadrats in each study site were measured and tagged with a unique number. All such trees were identified to species in the field or, if identification was not possible in the field, samples were collected for future identification.

Sampling of amphibians and reptiles was done by personnel walking trails in the study zones and in other areas both by day and night. Also five arrays of drift fences with pitfall traps were established in each quadrat system; each array consisted of 20 meters of aluminum fencing and five pitfall traps (Fig. 8). These traps were checked shortly after first light each morning, again shortly before dark, and usually again at night. In this way diel activity was ascertained. All individuals were recorded with respect to quadrat number and date; exclusive of specimens found in pitfall traps, all individuals observed also were recorded with respect to time, height above ground, and activity. Usually within a few hours after capture, specimens were weighed using Pesola scales; after specimens were anesthetized, tissues (usually striated muscle and liver) were preserved in liquid nitrogen. Specimens were then preserved in 10% formalin and subsequently transferred to 70% ethanol.

Unless noted otherwise in specific accounts, the taxonomy used herein follows Duellman (1993) for anurans and Peters and Donoso-Barros (1970) and Peters and Orejas-Miranda (1970) for squamates, except that for iguanians we follow Frost and Etheridge (1989) and Frost (1992), and for pitvipers Campbell and Lamar (1989). In the accounts of the species, all measurements are in mm and masses (weights) in grams. Measurements of anurans follow Duellman (1970); snout-vent length is abbreviated SVL. Measurements of squamates are given as SVL + tail length. Webbing formulae for anurans are based on Savage and Heyer (1967) as modified by Myers and Duellman (1982). Stomachs of all snakes were examined for the presence of prey items. The specimens were divided between the Natural History Museum at The University of Kansas (KU) and the Museo de Historia Natural, Universidad Ricardo Palma, Lima, Peru. Catalogue numbers have yet to be assigned to the latter specimens, so they are referred to by URP-WED field numbers. Other museum codes are: ANSP Academy of Natural Sciences, Philadelphia; BM Natural History Museum, London; MLS, Museo La Salle, Santa Fe de Bogotá, Colombia; MPEG Museu Paraense Emilio Goeldi, Belém, Brazil; RMNH Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands; USNM National Museum of Natural History, Washington; WCAB Werner C. A. Bokermann, São Paulo, Brazil.

Fig. 8. Aluminum drift fences and pitfall traps in Quadrat No. 6 in the study zone at San Jacinto. July 1993.

SPECIES ACCOUNTS

Families, genera, and species are arranged alphabetically within orders.

BUFONIDAE

Bufo marinus (Linnaeus)

At SJ, five juveniles and subadults were found in the camp clearing, and one gravid female having a SVL of 144.0 and a mass of 240 was in a pitfall trap in the forest about 5 m from the edge of the lagoon and about 50 m from the edge of the forest. A subadult male having a SVL of 80.0 and a mass of 44.0 was on the riverbank at night at TL.

Bufo typhonius Complex

The systematic status of the forest-dwelling toads generally referred to *Bufo typhonius* is under study by Marinus S. Hoogmoed, who recognizes at least seven sympatric species in the complex in eastern Ecuador and northern Peru (Hoogmoed, 1986). Three species were identified among the material collected at the study sites in northern Loreto, Peru. All three have the first and second fingers equal in length, lateral fringes on the fingers and toes, and the digital tips terminating in distinct, round, pads. Assignment of names to these species awaits the completion of Hoogmoed's studies. In the meantime, each taxon is discussed herein under alphabetical designations. The characters used to define each species are given in the same numerical order in each account.

Species A

This species can be defined as follows (n = 9 ♂♂, 9 ♀♀, 20 juveniles): (1) SVL ♂♂ 45.9–67.4 ($\bar{x}$ = 57.7), ♀♀ 48.0–76.0 ($\bar{x}$ = 59.6); (2) mass ♂♂ 9.0–26.3 ($\bar{x}$ = 15.0), ♀♀ 13.5–37.5 ($\bar{x}$ = 18.6); (3) snout pointed in dorsal view, greatly protruding beyond margin of lip, rounded above, and curved posteroventrally in profile; (4) nostrils protuberant dorsolaterally at point above anterior margin of lower jaw; (5) canthal, supraorbital, and supratympanic crests continuous; supratympanic crest greatly hypertrophied and expanded dorsolaterally in females; (6) tympanum round, distinct, 55–60% diameter of eye; (7) bony protrusion at angle of jaws small in males, large in females; (8) neural crests of vertebrae barely protruding in males, greatly protruding in females; (9) parotoid glands triangular, protruding laterally, incorporated into lateral row of tubercles; (10) lateral row of tubercles rounded in males and long, tubercles conical in females; (11) skin on dorsum smooth in males, tubercular in females; (12) skin on dorsal surfaces of limbs smooth in males, spinous in females; (13) palmar tubercle large, ovoid, 3 times size of subtriangular thenar tubercle; (14) inner metatarsal tubercle elliptical, twice size of ovoid outer metatarsal tubercle; (15) modal webbing on foot **I** 1—2 **II** 1—3 **III** $1\frac{1}{2}$—$3\frac{1}{2}$ **IV** $3\frac{1}{2}$—$1\frac{1}{2}$ **V**; (16) supernumerary tubercles large, round, nearly size of subarticular tubercles; (17) vocal slits and nuptial excrescences present in males.

In life, the dorsum varies from reddish brown to yellowish tan with or without markings consisting of small dark brown to black spots, large black mark in scapular region, or black snout (Fig. 9). The flanks are colored like, or are darker than, the dorsum. The lateral row of tubercles (and protruding neural spines in females) are pale tan to yellowish orange. The venter is orange-tan with varying amounts of dark gray mottling or gray with cream spots posteriorly.

This species was found at SJ, TL, and NTL. Most individuals were either active on the forest floor by day or found in pitfall traps by day; six adults and one juvenile were sleeping on vegetation 0.2–0.5 m above ground at night. Twenty juveniles have SVLs of 16.0–30.0 and masses of 0.1–1.6.

Species B

This species can be defined as follows (n = 2 ♂♂): (1) SVL ♂♂ 52.2–54.9 ($\bar{x}$ = 53.6); (2) mass ♂♂ 8.0–9.6 ($\bar{x}$ = 8.8); (3) snout pointed in dorsal view, greatly protruding beyond margin of lip, pointed above, and inclined posteroventrally in profile; (4) nostrils protuberant posterodorsally at point anterior to anterior margin of lower jaw; (5) canthal crest not elevated; supraorbital and supratympanic crests continuous; supratympanic crest not hypertrophied and expanded; (6) tympanum round, distinct, 55–60% diameter of eye; (7) bony protrusion at angle of jaws small; (8) neural crests of vertebrae barely protruding; (9) parotoid glands narrowly elliptical, not protruding laterally, incorporated into lateral row of tubercles; (10) lateral row of long, conical tubercles present; (11) skin on dorsum tubercular; (12) skin on dorsal surfaces of limbs spinous; (13) palmar tubercle large, round, four times size of subconical thenar tubercle; (14) inner metatarsal tubercle ovoid, twice size of round outer metatarsal tubercle; (15) modal webbing on foot **I** 1—2 **II** 1—3^- **III** 2^-—3^- **IV** 3^-—2^- **V**; (16) supernumerary tubercles moderate, subconical, about one half size of subarticular tubercles; (17) vocal slits present and nuptial excrescences absent in males.

In life, the dorsum is dark brown with diffuse slightly paler blotches and cream lateral tubercles (Fig. 9). The venter is dull cream with a gray suffusion on the throat and chest.

One individual was on the forest floor by day at SJ, and one was sleeping at night on a vine 2 m above the edge of a stream at night at TL.

Species C

This species can be defined as follows (n = 6 ♂♂, 10 ♀♀, 11 juveniles): (1) SVL ♂♂ 40.6–53.7 ($\bar{x}$ = 46.7), ♀♀ 46.0–56.7 ($\bar{x}$ = 51.3); (2) mass ♂♂ 3.6–13.0 ($\bar{x}$ = 7.8), ♀♀ 6.0–14.0 ($\bar{x}$ = 10.3); (3) snout pointed in dorsal view, greatly protruding beyond margin of lip, pointed above, and inclined posteroventrally in profile; (4) nostrils protuberant posterodorsally at point anterior to anterior margin of lower jaw; (5) canthal crest not elevated; supraorbital and supratympanic crests continuous; supratympanic crest hypertrophied and slightly flared laterally in both sexes; (6) tympanum round, indistinct posteriorly, 75–80% diameter of eye; (7) bony protrusion at angle of jaws absent; (8) neural crests of vertebrae not protruding; (9) parotoid glands narrowly elliptical, not protruding laterally, incorporated into lateral row of tubercles; (10) lateral row of conical tubercles present; (11) skin on dorsum tubercular; (12) skin on dorsal surfaces of limbs spinous; (13) palmar tubercle large, ovoid, three times size of elliptical thenar tubercle; (14) inner metatarsal tubercle ovoid, half again size of ovoid outer metatarsal tubercle; (15) modal webbing on foot **I** 1—2 **II** 1—3^- **III** 1—$3\frac{1}{2}$ **IV** $3\frac{1}{2}$—1 **V**; (16) supernumerary tubercles large, subconical, nearly size of subarticular tubercles; vocal slits and nuptial excrescences absent in males.

The dorsum varies from grayish tan to reddish tan with darker brown markings, usually in the form of a broad middorsal mark with irregular edges; other individuals have only a few dark brown spots on the dorsum (Fig. 9). A middorsal cream stripe is present in some specimens. The spines in the lateral row are tan. The venter varies from gray with cream spots to orange-tan with gray mottling.

This species was found at SJ, TL, and NTL. One juvenile and 11 adults were sleeping on vegetation 0.2–1.0 m above ground at night; the others were on the forest floor or in pitfall traps by day. Two recently metamorphosed young from TL have SVLs of 5.8 and 6.7, and masses of < 0.1.

Dendrophryniscus minutus (Melin)

Of nine adults and three juveniles, all were found amid leaf litter on the ground by day in the floodplain forest at TL, except one male was on the shore of the oxbow lake at night. Three males have SVLs of 15.3–17.7 ($\bar{x}$ = 16.8) and masses of 0.4–0.5 ($\bar{x}$ = 0.43); six gravid females have SVLs of 17.3–19.4 ($\bar{x}$ = 18.4), and masses of 0.3–0.7 ($\bar{x}$ = 0.45). Three juveniles have SVLs of 7.8–10.2 ($\bar{x}$ = 8.8) and masses of < 0.1. The venter is reddish purple; all except one male have orange spots on the belly.

DENDROBATIDAE

Colostethus trilineatus (Boulenger)

Seven individuals were active in thick leaf litter in flood-

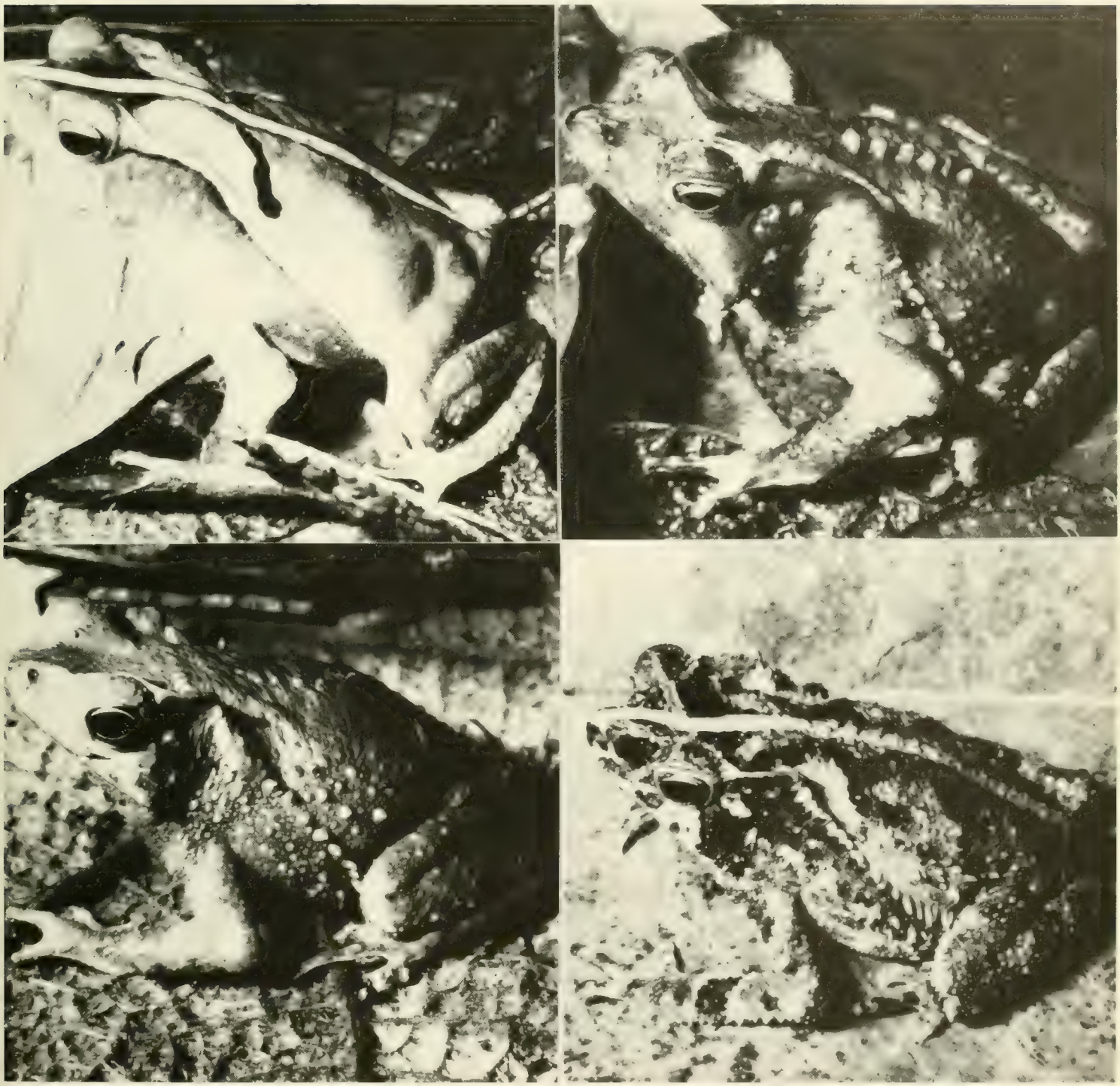


Fig. 9. *Bufo typhonius* complex. Top left—Species A, KU 221794, adult male, 53.5 mm SVL. Top right—Species A, KU 221793, adult female, 58.5 mm SVL. Bottom left—Species B, KU 221810, adult male, 52.2 mm SVL. Bottom right—Species C, KU 222326, adult female, 55.0 mm SVL.

plain forest at TL on 22 and 23 July. One male has a SVL of 13.9 and a mass of 0.15, and three females have SVLs of 15.8–16.1 ($\bar{x}$ = 15.9) and masses of 0.2–0.3 ($\bar{x}$ = 0.25); two juveniles have SVLs of 10.5 and 11.7 and masses of 0.1 each. In life, the dorsum is brown with a broad tan dorsolateral stripe, below which the flanks are black; the labial and ventrolateral stripes are white; the throat and belly are pale yellow. The undersides of the hind limbs are pale gray, and there is a pinkish tan diagonal mark on the proximal posteroventral surfaces of each thigh. The iris is deep bronze heavily flecked with black.

These specimens are tentatively assigned to this species, which was recognized as distinct from *C. marchesianus* (Melin) by Morales (1994). Upon examining the holotype of *C. trilineatus* (BM 1947.2.14.20), Morales (1994:101) observed "...la presencia de una línea ventrolateral, una línea vertebral fina, una línea labial, una garganta obscura y un tercer dedo manual del macho dilatado." Morales (1994) noted that *C. marchesianus* lacks a vertebral line and males do not have a dark throat; these are the only characters that he gave for distinguishing the two species, neither of which he compared with his new species, *C. juanii*, from Meta, Colombia. However, in the diagnosis of *C. juanii*, it is mentioned that a dorsolateral line is absent, and males do not have a dilated third finger. Among the 42 specimens of *C. trilineatus* that Morales listed from Amazonian Peru are KU 205270–82 and 207547–49 from Cuzco Amazónico, Departamento Madre de Dios, Peru. Assuming those specimens to represent *C. trilineatus*, we prepared a full diagnosis with number characters following the format of Duellman and Simmons (1988).

Diagnosis.—A small species of *Colostethus* characterized by (1) small size, SVL in males 15.1–17.2 ($\bar{x}$ = 16.0, n = 6), in females 15.6–18.5 ($\bar{x}$ = 16.8, n = 10); (2) disc on third finger slightly wider than diameter of finger; (3) first finger much longer than second; (4) fringe absent on second finger; (5) disc on fourth toe much wider than diameter of toe; (7) outer tarsal fold absent; (8) toes unwebbed; (9) dorsolateral stripe present; (10) oblique lateral stripe short, diffuse, and indistinct (n = 13) or absent (n = 3); (11) ventrolateral stripe present, continuous with labial stripe; (12) dark markings absent on chest; (13) dark markings absent on belly; (14) throat gray in males, cream in females; (15) third finger of males not dilated.

It is evident that these specimens that were assigned to *C. trilineatus* by Morales (1994) do not agree in all respects with the characters that he listed for the holotype from Yurimaguas, Peru. Only seven of the 16 specimens have a narrow, pale vertebral line, and none of the males exhibits a swollen third finger. Likewise, the presence of an oblique lateral stripe is variable.

The specimens from TL closely resemble the specimens from Cuzco Amazónico. A pale vertebral line is diffuse in one individual and absent in the others. The oblique lateral stripe is short and diffuse in three individuals and longer and distinct in three others. The only male is a subadult, so throat color and condition of the third finger cannot be determined.

Dendrobates ventrimaculatus Shreve

This small, diurnal species was found on the forest floor at the SJ and NTL study zones and on the floodplain at TL. One female with small ovarian eggs has a SVL of 15.7 and a mass of 0.2; four males have SVLs of 13.0–15.5 ($\bar{x}$ = 14.5) and masses of 0.1–0.2 ($\bar{x}$ = 0.18). All specimens have a distinct inner metatarsal tubercle. In life, the throat is black with a pale spot; the belly and ventral surfaces of the limbs are blue with large black spots, and the other surfaces of the limbs are black with blue reticulations. The dorsal stripes and spot on the chin are pale golden yellow in the female and bright orange in males. The posterior extent of the middorsal stripe is variable—to the scapular region in one, to the sacrum in two, and nearly to the posterior end of the body in two. In one of the specimens in which the stripe extends to the sacrum, the dorsum postsacrally has fine blue reticulations; in the other specimens reticulations are absent on the dorsum of the body.

Dendrobates ventrimaculatus has only recently been resurrected from the synonymy of *D. quinquevittatus* Steindachner and recognized as a possible complex of species (Caldwell and Myers, 1990). The present specimens agree with those described and illustrated (as *D. quinquevittatus*) by Meede (1980) from Panguana, Peru, and the four males agree with the color photograph of an individual from Ecuador (Lötters, 1988). Furthermore, they agree with a specimen (KU 220870) from the junction of the Río Yanamono and Río Amazonas, Departamento Loreto, Peru, in color pattern and in having orange stripes on the dorsum. However, they differ from specimens (reported as *D. quinquevittatus*) from Lago Agrio, Ecuador, which have yellow reticulations on the limbs (Duellman, 1978).

Epipedobates femoralis (Boulenger)

One adult male having a SVL of 27.3 and a mass of 1.5 was on the forest floor by day in the study zone at SJ. Four juveniles having SVLs of 13.5–18.2 ($\bar{x}$ = 14.9) and masses of 0.1–0.2 ($\bar{x}$ = 0.17) and one adult male having a SVL of 29.9 and a mass of 2.4 were on the forest floor by day in the study zone at NTL. The latter, found on 23 July, was carrying eight tadpoles in Stage 28 (Gosner, 1960). The tadpoles have body lengths of 4.0 mm and total lengths of 11.5 mm; the second lower and third lower tooth rows are partially developed, whereas the other rows are well developed. The body is black, and the tail creamy tan with small brown spots.

Epipedobates hahneli (Boulenger)

One juvenile male having a SVL of 19.5 and a mass of 0.5 was sleeping on a leaf 1 m above the ground at night in the study zone at SJ. We follow Haddad and Martins (1994) in recognizing this species as distinct from *Epipedobates pictus*.

Epipedobates zaparo (Silverstone)

In the study zones at SJ and NTL, 12 individuals were on

the forest floor and in pitfall traps by day and six were sleeping on low vegetation (0.1–0.7 m) at night. Six males have SVLs of 20.7–22.3 ($\bar{x}$ = 21.4) and masses of 0.6–0.9 ($\bar{x}$ = 0.7); ten females have SVLs of 23.3–27.1 ($\bar{x}$ = 25.4) and masses of 0.7–1.2 ($\bar{x}$ = 1.08). In life, the dorsum is dark red, and the venter is blue and black.

These specimens represent the second and third recorded localities of the species in Peru and the first localities outside the Río Pastaza drainage. Henle (1992) reported it from Capahuari Sur in the Río Pastaza drainage, the same drainage as all Ecuadorian localities for the species (Silverstone, 1976). Capahuari Sur is approximately 40 km SSW of Teniente López and 80 km SW of San Jacinto. Schulte's (1987) record of *E. zaparo* from Departamento San Martín, Peru, was based on specimens subsequently named *Epipedobates cainarachi* (Schulte, 1989) and *Epipedobates ardens* (Jungfer, 1989).

HYLIDAE

Hyla albopunctulata Boulenger

One male having a mass of 1.3 was on the top panel of a mist net (2 m above the ground) on the night of 1 July in the study zone at SJ. Comparison of this specimen with Boulenger's (1882) description and detailed notes on, and photographs of, the type series indicate that the present specimen (KU 221849) represents the rediscovery of this species.

The syntypes are BM 80.12.5.159–162 from "Ecuador" and 80.12.5.230 from "Sarayacu"; all were collected by Buckley. When the syntypes were examined on 16 June 1969, all were in the same jar; BM 80.12.5.159 and 230 had tags attached; the other three specimens were untagged. All of the specimens were soft and somewhat faded. Three males (BM 80.12.5.159, 230, and an untagged specimen) having many small white spots on the dorsum have SVLs of 32.2, 35.6, and 31.0, respectively. Because this species has not been identified with populations in the Amazon Basin, a redescription is provided.

Description.—n = 1 male. Body moderately slender, not as wide as head; snout long, rounded in dorsal view, slightly inclined posteroventrally in profile; canthus rostralis curved, rounded in section; loreal region barely concave; lips thin, moderately flared anterior to orbits; top of head flat; internarial region depressed; nostrils protuberant, directed dorsolaterally at level of anterior margin of lower jaw; eye directed anterolaterally (35° to longitudinal axis); supratympanic fold diffuse, obscuring upper one third of tympanum; tympanic annulus weak; tympanum directed dorsolaterally, separated from orbit by distance 1.5X tympanum.

Forearm moderately robust with ulnar keel continuous with narrow fringe on outer edge of Finger IV; fingers long with round terminal discs; diameter of disc on third finger equal to three fourths diameter of tympanum; relative lengths of fingers I < II < IV < III; fingers webbed basally and bearing narrow lateral fringes; webbing formula for fingers **II** 2^{+}—3 **III** 3—$2\frac{1}{2}$ **IV**; subarticular tubercles moderately large, round, elevated; distal tubercle on Finger IV bifid; supernumerary tubercles absent; palmar tubercle small, round; thenar tubercle large, rectangular; nuptial excrescences absent. Hind limb slender; calcars and heel tubercles absent; inner tarsal fold thin, extending full length of tarsus; outer metatarsal tubercle absent; inner metatarsal tubercle ovoid, visible from above; toes long, bearing discs slightly smaller than those on fingers; relative lengths of toes I < II < III < V < IV; toes about three-fifths webbed; webbing formula **I** 2^{-}—2^{+} **II** 1—2+ **III** 1—3^{-} **IV** 2^{-}—1 **V**; subarticular tubercles large, round, elevated; supernumerary tubercles absent.

Skin on dorsum smooth; skin on belly and ventral surfaces of thighs granular; other surfaces smooth; cloacal opening directed posteroventrally at midlevel of thighs; cloacal sheath short; cloacal folds and tubercles absent. Dentigerous processes of vomers long, narrowly separated medially, inclined posterolaterally between posterior margins of choanae, each bearing nine teeth. Choanae large, elliptical; tongue broadly cordiform, shallowly notched posteriorly, barely free behind. Vocal slit elongate from midlateral base of tongue to angle of jaw; vocal sac single, median, subgular.

Color in preservative: Dorsal surfaces of head, body, and limbs purplish brown (under 10X magnification cream with dense chromatophores on head and body and scattered chromatophores on limbs); discs on digits, margin of upper lip, venter, and hidden surfaces of limbs pale creamy white.

Color in life: At night, pale purple; by day, pale dull green changing to dull tan on dorsum; pale purple on venter and hidden surfaces of limbs; peritoneum white; iris silvery bronze (Pl. 1).

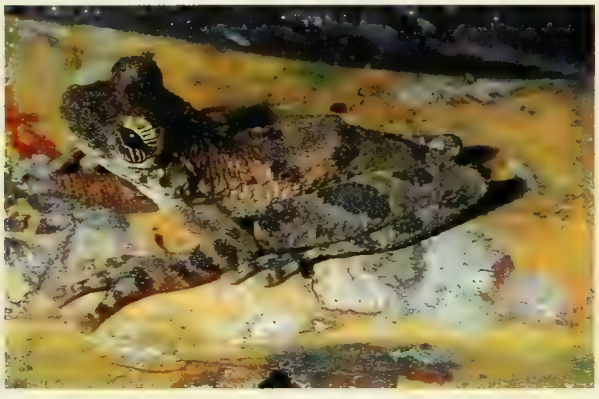
Measurements: SVL 31.6, tibia length 15.8, foot length 12.1, head length 11.8, head width 11.0, interorbital distance 3.0, upper eyelid 2.4, internarial distance 1.9, eye-nostril 3.7, eye 2.8, tympanum 1.5.

Remarks.—The present specimen is the first record of the species from Peru; the only other definite localities are Sarayacu, Provincia Pastaza (BM 80.12.5.159–162), and San Pablo Kantesyia, Provincia Napo (KU 221637), Ecuador. The latter specimen is an adult female having a SVL of 30.2 mm. The apparent rarity of this species having a distribution encompassing about 300 km in latitude in the upper Amazon Basin may indicate that it is an inhabitant of the canopy and perhaps breeds in bromeliads. The only reference, other than in checklists, to this species is by Cochran and Goin (1970). As pointed out by Myers and Duellman (1982), Cochran and Goin (1970) erroneously placed *Hyla palmeri* Boulenger 1908, in the synonymy of *Hyla albopunctulata* and based their description of the latter species on a specimen of the former. Frost (1985) commented that *Hyla albopunctulata* questionably is in the *Hyla bogotensis* group. After examining the present specimen, this suggestion lacks merit; the relationships of *H. albopunctulata* are unclear, but it does not seem to be associated with the *Hyla bogotensis* group, adult males of which have a mental gland and proportionately more robust bodies and limbs. Only one of the specimens in the type series of *H. albopunctulata* has small white spots on the dorsum. Boulenger's (1882) description does not agree in all respects with his illustration (Plate XXIV, Fig. 4) or with the specimen (unlabelled, but with white spots) that he described and illustrated. He stated that the head is wider than long; my measurements of the specimens indicate the opposite. Boulenger stated that the outer fingers were one-half webbed and the toes fully webbed; his illustration shows the fingers to be no more than one-third webbed and the toes no more than two-

PLATE 1

Hyla albopunctulata, KU 221849, male, 31.6 mm SVL.

Phyllomedusa hulli, URP-WED 60198, male, 37.1 mm SVL.



Osteocephalus buckleyi, KU 221926, female, 50.0 mm SVL.

Osteocephalus cabrerai, KU 221927, female, 41.0 mm SVL.

Eleutherodactylus delius, URP-WED 59957, female, 30.9 mm SVL.

Eleutherodactylus luscombei, KU 222002, female, 26.1 mm SVL.

Adelophryne trudactyla, KU 221992, female, 11.5 mm SVL.

Microhylid, KU 222108, female, 17.8 mm SVL.

thirds webbed; the degree of webbing was confirmed to be correct in the illustration.

Hyla boans (Linnaeus)

A gravid female having a SVL of 106.3 and a mass of 67.0 was on the ground in the camp clearing at SJ at 0615 h on 3 July. On the night of 18 July at TL several males were calling from boulders in, and trees along, a clear stream with sandy banks. The one male collected has a SVL of 113.5 and a mass of 31.0 g.

Hyla brevifrons Duellman and Crump

Three males were calling from emergent vegetation 1.0–1.5 m above the surface of the temporary pond at TL on the night of 22 July. These specimens have SVLs of 16.0–16.3 ($\bar{x}$ = 16.1) and masses of 0.2–0.3 ($\bar{x}$ = 0.27); they agree in color and external morphology with the description of Duellman and Crump (1974).

Hyla calcarata Troschel

With the exception of a single male having a SVL of 34.7 and a mass of 2.2 on a branch of a bush 0.5 m above the edge of the oxbow lake at TL on 24 July, all individuals were found at the edge of a black-water lagoon at SJ on the nights of 30 June–5 July. Individuals were perched perpendicularly on vines or branches of bushes 0.1–2.0 m above the edge of the lagoon. No calls were heard. Of the specimens from SJ, two gravid females have SVLs of 49.6 and 54.3 and masses of 4.3 and 4.8; 17 males have SVLs of 35.4–40.5 ($\bar{x}$ = 38.4) and masses of 1.9–2.8 ($\bar{x}$ = 2.38).

Hyla fasciata Günther

One male was perched on a vine 0.2 m above a small stream in the study zone at NTL on the night of 23 July; 11 males were on reeds and bushes in the swamp at SJ on the nights of 7–11 July. These 12 males have SVLs of 30.1–33.5 ($\bar{x}$ = 31.4) and masses of 1.2–2.0 ($\bar{x}$ = 1.36).

Hyla geographica Spix

With the exception of one nongravid female having a SVL of 55.5 and a mass of 6.2 on a limb of a tree 3 m above the ground in primary forest at NTL on the night of 16 July and a gravid female on the limb of a bush 1.5 m above the stream at TL on the night of 22 July, all individuals were on low vegetation (0.5–0.7 m) at the edge of permanent water at night—one male in the swamp at SJ on 7 July and one female and seven males at the oxbow lake at TL on 24 and 25 July. Eight males have SVLs of 40.9–51.0 ($\bar{x}$ = 44.8) and masses of 2.3–5.5 ($\bar{x}$ = 3.68); two gravid females have SVLs of 65.2 and 68.7 and masses of 13.5 and 19.5.

Color notes on a nongravid female (KU 221870): Dorsum tan with dark brown and pale cream marks; flanks and hidden surfaces of thighs bluish gray with black vertical marks; venter deep yellow with brown spots on belly; iris orange-brown; palpebrum reticulate. In contrast, a male (KU 221869) had the belly and undersides of the limbs orange, and the flanks orange with brown bars. All but three individuals have pale spots on the dorsum. One female (KU 221871) has four large and two small spots on the dorsum and white heels; two females and five males have 1–8 small white spots on the dorsum; three of these have white heels, and in one specimen the white is restricted to the calcars. The coloration and structure of these specimens agrees with the detailed descriptions given by Duellman (1973a, 1978).

A large school of tadpoles was observed in the oxbow lake at TL on 23 July. A sample of 25 individuals agrees with the description provided by Hero (1990). The sample contains specimens in Stages 31–33 (Gosner, 1960) having body lengths of 13.8–16.5 ($\bar{x}$ = 14.9) and total lengths of 34.9–41.5 ($\bar{x}$ = 37.8). These tadpoles are uniform black and have a labial tooth row formula of 3/5; the first upper row is just inside the fringing papillae, is made up of small teeth, and is interrupted medially, as is the third upper row. The first lower row is shorter than the others, and the fifth row is incomplete and made up of small teeth.

Hyla granosa Boulenger

Males were calling from leaves 3–10 cm above the water at the edge of the lagoon and in the swamp at SJ nearly every night between 30 May and 11 July. Four males have SVLs of 33.6–36.1 ($\bar{x}$ = 34.9) and masses of 2.0–2.5 ($\bar{x}$ = 2.18). A metamorphosing young having a SVL of 12.0 was on an emergent reed in the open pond on 9 July. In life, the dorsum and venter of the young individual were pale green; faint reddish brown canthal and postorbital stripes were evident. The digits were pale yellow, and the iris was creamy yellow.

Hyla koechlini Duellman and Trueb

Males were calling from low vegetation (< 1.0 m) at the edge of a pond in primary forest at NTL on the nights of 20 and 24 July. Another male was on the leaf of a tree 2 m above the ground near the same pond on the night of 22 July, and a gravid female was on low vegetation at the edge of the pond on 20 July. The gravid female has a SVL of 25.4 and a mass of 1.3; eight males have SVLs of 19.5–22.0 ($\bar{x}$ = 20.8) and masses of 0.4–0.6 ($\bar{x}$ = 0.53). The female has black thighs and anterior and posterior surfaces of the thighs, whereas the flanks in the males are brown. One male has two pale spots on the anterior surfaces of the thighs, and two others each have one spot. These specimens agree with the large type series described by Duellman and Trueb (1989) and provide a range extension of about 1250 km to the NNW of the previously reported northernmost specific locality, Cocha Cashu, Madre de Dios, Peru (Rodríguez, 1992), although Rodríguez and Duellman (1994) included the species in a guide to the frogs of the Iquitos region of Peru.

Hyla lanciformis (Cope)

This large treefrog was common at the margins of the lagoon and in the swamp at SJ, where males were calling from bushes and trees 0.5–1.0 m above the ground or water nearly every night between 30 May and 11 July. Two males were found more than 100 m away from water; one was on the leaf an *Aechmea* at night, and the other was caught in a Sherman live trap on a branch 1.5 m above the ground. Two individuals were perched on low trees in the forest at TL, and one was on a stick 1 m above the ground at night at NTL. Three adult females have SVLs of 71.0–78.4 ($\bar{x}$ = 73.7) and masses of 19.5–23.0 ($\bar{x}$ = 21.5); 13 adult males have SVLs of 52.9–71.2 ($\bar{x}$ = 62.2) and masses of 8.9–20.0 ($\bar{x}$ = 13.2). Two subadult females and one subadult male have SVLs of 56.1, 53.4, and 46.3 and masses of 10.0, 7.0, and 4.6, respectively. Three juveniles from SJ have SVLs of 24.6–38.7 ($\bar{x}$ = 30.6) and masses of 0.6–3.1 ($\bar{x}$ = 1.5). Two tadpoles in Stage 34 (Gosner, 1960), having body lengths of 8.7 and 9.0 and total lengths of 26.0 and 27.4, were in the swamp at SJ on 11 July. In life, they were pale tan with brown spots on the tail; they agree with the description provided by Duellman (1978). Two metamorphosing young, having SVLs of 14.0 and tail stubs of 1.5, were on reeds in the same pond on 9 July. The presence of calling males, gravid females, tadpoles, metamorphosing young, and juveniles of a wide range in size suggests that the breeding season is long.

Hyla leucophyllata (Bereis)

One female was on a leaf 1.0 m above the ground at night at TL, and all other individuals are from study zone at SJ, where a female was on a leaf 3 m above the ground at night and males were calling from leaves and branches of bushes 0.5–2.0 m above the edge of the lagoon on the nights of 2–11 July. Ten males have SVLs of 22.9–25.1 ($\bar{x}$ = 23.9) and masses of 0.6–1.1 ($\bar{x}$ = 8.8), and two gravid females have SVLs of 31.7 and 31.9 and masses of 2.4 and 2.9 g.

Hyla marmorata (Laurenti)

A gravid female having a SVL of 46.1 and a mass of 3.9 was perched on a fern at the edge of the forest at NTL on 18 July.

Hyla parviceps Boulenger

On 20 July, three males were observed leaping from leaf to leaf toward the forest pond at NTL at 2230 h; there had been a light rain just before dusk. No calling males were observed that night, but, on 21–24 July, males were calling from low vegetation in, and around the pond. On 22 July, males were calling from emergent vegetation in the temporary pond at TL. One gravid female was at the former pond on 21 July, and one spent female was on a branch of a tree 4 m above ground away from the pond. Two females have SVLs of 21.4 and 22.1 and a masses of 0.7 (gravid) and 0.5 (spent), respectively; 10 males have SVLs of 15.4–17.9 ($\bar{x}$ = 16.7) and masses of 0.2–0.3 ($\bar{x}$ = 0.23). In life, the spots on the ventral surfaces of the arms and shanks are bright orange; the posterior part of the belly and ventral surfaces of the thighs are pale blue with black markings, and the spots on the flanks are white.

Hyla rhodopepla Günther

Males were calling from emergent vegetation in the forest pond at NTL on 20 July. Thirteen males have SVLs of 19.4–21.8 ($\bar{x}$ = 20.8) and masses of 0.5–0.7 ($\bar{x}$ = 6.38). In preservative, four specimens have reddish brown spots on the dorsal surfaces of the head, body, and shanks; the others are uniform creamy yellow.

Hyla riveroi Cochran and Goin

Males were calling from leaves of bushes and trees 0.5–1.5 m above the water in the swamp at SJ on 7 and 9 July and from leaves of bushes at the edge of the temporary pond at TL on 22 and 24 July. Seven males have SVLs of 15.6–17.5 ($\bar{x}$ = 16.7) and masses of 0.2–0.3 ($\bar{x}$ = 0.26); two females have SVLs of 17.8 and 18.0 and mass of 0.3. Living individuals at night were pale reddish brown with a dark brown dorsolateral stripe and yellow vocal sac; by day, the dorsum was creamy tan with or without brown markings and a cream suborbital spot. In preservative, all specimens have dark brown canthal and postorbital stripes that extend to the midflank and a cream labial stripe (fragmented in two specimens). A dark brown interorbital bar is present in six specimens, and four have a middorsal dark stripe extending to the sacrum; this stripe is continuous with the interorbital bar in three specimens. One female (URP-WED 60484) deposited a clutch of 34 unpigmented eggs in a single layer of clear gelatin on the inside of a plastic bag.

Hyla sarayacuensis Shreve

Except for one male on the leaf of a bush 0.5 m above the ground at in the study zone at TL, all individuals were found at the temporary pond at NTL. One male was on a leaf by day, and all others were calling from leaves of bushes 0.5–1.0 m above the edge of the pond on the nights of 20 and 24 July. One postpartum female has a SVL of and a mass of 2.3; 23 males have SVLs of 24.4–28.7 ($\bar{x}$ = 25.9) and masses of 0.7–1.2 ($\bar{x}$ = 0.91).

Osteocephalus Steindachner

Generally four species of *Osteocephalus*—*buckleyi* (Boulenger), *leprieurii* (Duméril and Bibron), *subtilis* Martins and Cardoso, and *taurinus* Steindachner—are recognized to occur in the upper Amazon Basin, and three additional species—*O. elkejungingerae* (Henle), *pearsoni* (Gaige), and *verruciger* (Werner)—are recognized on the Amazonian slopes of the Andes (Duellman, 1993). Close examination of the material collected in northern Peru reveals the existence of six species in the Amazon lowlands in Departamento

Loreto. In addition to the three species usually recognized there, there are two others for which names placed in the synonymies of *O. buckleyi* and *O. taurinus* by Trueb and Duellman (1971) are available. Another small species that breeds in bromeliads remains unnamed. An even smaller species, *O. rodriguezi* (Rivero) from the Guiana Highlands (Duellman and Hoogmoed, 1992) is now placed with five other small species from the Guiana Highlands in the genus *Tepuihyla* (Ayarzagüena et al., 1992).

Osteocephalus buckleyi (Boulenger)

One female (KU 221926) with flaccid, empty oviducts has a SVL of 50, and a mass of 5.4; it was on a branch of a bush about 1 m above the ground at night on 17 July in the study zone at NTL. In life, the dorsum was tan with brown blotches on the body and brown transverse bars on the limbs; the shanks were pale brown with distinct dark brown bars, and the anterior and posterior surfaces of the thighs were brown (Pl. 1). The throat and belly were cream with small brown spots, and the ventral surfaces of the hind limbs were tan. The margin of the upper lip was bronze-tan, and the iris was bronze with radiating black lines and a broad, median, horizontal reddish brown streak. The measurements and proportions, as well as the general features of structure and coloration, agree well with the type series (see Trueb and Duellman, 1971). The skin on the anterior part of the flank is distinctly areolate, and the axillary membrane is short and thick. The webbing formula for the hand is **II** $1\frac{1}{2}$—$1\frac{1}{2}$ **III** 2^{+}—2^{+} **IV** and for the foot **I** 1—1 **II** 1—2^{-} **III** 1—$1\frac{1}{2}$ **IV** $1\frac{1}{2}$—1 **V**.

Osteocephalus cabrerai (Cochran and Goin)

New combination

In their description of *Hyla cabrerai*, Cochran and Goin (1970) stated that the species was most closely related to *Hyla* (= *Osteocephalus*) *buckleyi*. The type locality—Caño Guacayá, tributary of the lower Río Apaporis, Departamento Amazonas, Colombia—is in the Amazon Basin east of northern Peru. This name was synonymized with *O. buckleyi* by Trueb and Duellman (1971). A single female (KU 221927) with small ovarian eggs and a mass of 3.1 was perched on a bush in the swamp at SJ on the night of 10 July. This individual is sufficiently different, especially in the coloration of the eye, to distinguish it from *O. buckleyi*. Comparison of this specimen with data on, and photographs of, the holotypes of the species synonymized with *O. buckleyi* by Trueb and Duellman (1971), revealed a striking similarity with the holotype of *Hyla cabrerai* (USNM 152759, a female).

Following are the characteristics of KU 221927 with characteristics of the holotype in parentheses: SVL 41.0 (52.7), tibia length 21.5 (31.0), head length 14.1 (18.3), head width 14.7 (19.2), eye 4.6 (5.2), tympanum 4.0 (4.0), webbing on hand **II** 2^{-}—3^{-} **III** $2\frac{1}{3}$—2^{+} **IV** (**II** $1\frac{1}{2}$—2^{+} **III** 2^{+}—$1\frac{1}{3}$ **IV**), webbing on foot **I** 1—2^{-} **II** 1—2 **III** 1—2 **IV** 2—1 **V** (**I** 1—1^{+} **II** 1—$1\frac{1}{2}$ **III** 1—2^{-} **IV** 2^{-}—1 **V**); vomerine teeth 9–8 (9–10). In both individuals the snout is truncate in dorsal view, the nostrils protrude dorsolaterally, the supratympanic fold is tubercular, an axillary membrane extends to about the midlength of the upper arm, the digital discs are large and round (diameter of disc on third finger about two thirds diameter of tympanum), and rows of tubercles are present on the ventrolateral edges of the forearms and tarsi.

Structurally, the two specimens exhibit few differences. The dorsal skin is more tuberculate in the holotype, which has a weak inner tarsal fold that is lacking in KU 221927. The distal subarticular tubercle is bifid in the holotype and not in the other specimen. The nature of the dorsal skin and tarsal fold may be artifacts of preservation. The holotype evidently was dropped into preservative, whereas KU 221927 was laid out in a pan; the latter method tends to obscure tarsal folds. The nature of the distal subarticular tubercle on the fourth finger is variable in species of *Osteocephalus* (Trueb and Duellman, 1971). The holotype is larger and has slightly more webbing than KU 221927, but webbing is known to increase with size (Duellman, 1970).

The color pattern of the preserved specimens is nearly identical. Coloration in life of the holotype is unknown; color notes on KU 221927 when it was alive are: dorsum dark green with dark brown markings, viz., irregular interorbital bar, paired diagonal marks on occiput, transverse spot in cervical region, longitudinal marks on trunk, paired triangular marks in sacral region, transverse bars on limbs, and small labial spots (Pl. 1); flanks and ventral surfaces of limbs purplish brown; venter pinkish gray; posterior surfaces of thighs dark brown; tympanum copper; iris creamy orange.

Cochran and Goin (1970) designated two paratypes: WCAB 13284 from Amapá, Brazil and C. J. Goin 2317 from Vaupés, Colombia. The former is an example of *O. buckleyi;* the latter was not examined by Trueb and Duellman (1971). William W. Lamar collected one individual (not sexed) in Vaupés, Colombia; he compared it with the holotype of *O. cabrerai* and found them to be identical. He provided (W. W. Lamar: in lit.) the following field notes: "Collected 26 April 1979, along Caño Yapui (= Monserero), a tributary of Caño Tí, which feeds the Vaupés River from the south. Collected by day on a twig next to wet bank over water. Color in life: when collected by day it was pale chartreuse and pale grey-beige which, combined with the warty skin gave the impression of lichen. By night the chartreuse areas became rich lime-green and all beige regions changed to deep maroon-brown. Iris bronzy-gold; eyelid with fine red-gold reticulations. Tympanum copper colored; digits also. Dorsal pattern complex, reticulate. Legs and thighs with three bars each. Pinkish white anal and heel tubercles and tarsal ridge. Ventrally dirty white, heavily spotted on upper chest and below mandible with maroon-brown becoming suffused cloudy tan from lower abdomen to thighs and legs. Warty tubercles along outer edge of hand and forearm to elbow. Bones green. SVL = 62.4 mm."

The major difference between the specimen from SJ and the one from Caño Yapui is in the apparent color of the iris, which can change with light intensity. The principal aspect

of coloration of the iris in *O. cabrerai* is the absence of radiating dark lines. Most other *Osteocephalus* have a bronze or greenish yellow iris with radiating black lines. *Osteocephalus elkejungingerae* from the lower slopes of the Andes in Peru has a dull red iris, but it is larger and has different coloration than *O. cabrerai* (Henle, 1992).

Osteocephalus leprieurii (Duméril and Bibron)

One male is from the study zone at SJ; two females and eight males are from the study zone at NTL. All were found at night; one male was on the forest floor; all other individuals were on stems of saplings and bushes or on branches of trees, 0.5–2.5 m above the ground. Nine males, all with keratinized nuptial excrescences, have SVLs of 44.2–50.1 ($\bar{x}$ = 47.0) and masses of 4.3–6.4 ($\bar{x}$ = 5.3); two gravid females have SVLs of 62.6 and 67.0, and masses of 14.0 and 17.6, respectively. Color notes on two living individuals (KU 221929, ♂, and 221930, ♀) are: Dorsum olive-tan with brown transverse marks on body and limbs; flanks cream with extension of dorsal transverse brown marks; anterior and posterior surfaces of thighs brown; narrow cream line above cloacal opening and on heel; venter pale tan; labial stripe cream; iris creamy tan with black flecks; bones green. The supracloacal stripe is absent in one individual and interrupted medially in two specimens. The venters are immaculate, except in one male that has brown flecks on the throat and another that has brown flecks on the chest. The webbing formula for the two outer fingers is **III** $2\frac{1}{2}$—$(2–2\frac{1}{2})$ **IV** and for the fourth toe, $1\frac{1}{2}$—2^{-}.

These specimens agree well with the detailed description of this species provided by Trueb and Duellman (1971) and Duellman (1978) except for some measurements and proportions. One female (KU 221930) having a SVL of 67.0 is larger than the previously reported maximum size of 64.0, and one male (KU 221931) having a SVL of 50.1 is larger than the previously reported maximum size of 49.0 (Duellman, 1978). Tibia length/SVL of nine males is 0.526–0.597 ($\bar{x}$ = 0.553) in contrast to 0.514–0.571 ($\bar{x}$ = 0.538) for 21 males given by Trueb and Duellman (1971). The range of variation of head width/SVL falls within the range given by Trueb and Duellman (1971), but head length is proportionately greater in all males—0.349–0.370 ($\bar{x}$ = 0.358, n = 8) in contrast to 0.308–0.357 ($\bar{x}$ = 0.335, n = 21) (Trueb and Duellman, 1971). The smallest male (URP-WED 60149) with a SVL of 44.2 has a proportionately large head—head length/SVL 0.414, head width/SVL 0.394. Also, our specimens have a greater tympanum/eye ratio—0.820–0.910 ($\bar{x}$ = 0.862, n = 9 ♂♂) and 0.855–0.875 ($\bar{x}$ = 0.865, n = 2 ♀♀) and in contrast to 0.652–0.884 ($\bar{x}$ = 0.777, n = 21 ♂♂) and 0.698–0.909 ($\bar{x}$ = 0.785, n = 21 ♀♀) (Trueb and Duellman, 1971).

Osteocephalus planiceps Cope

This name is resurrected from the synonymy of *Osteocephalus taurinus* Steindachner, 1862 (synonymy fide Trueb and Duellman, 1971). Cope (1874) based the description of *Osteocephalus planiceps* on a single specimen (ANSP 11399) from Nauta, Departamento Loreto, Peru. The following diagnosis uses the numerical characters equivalent to those by Trueb and Duellman (1971): (1) Size large, sexual dimorphism moderate; maximum observed SVL in males 65.9, in females 85.9; (2) skin on dorsum in males bearing numerous, spinous tubercles, all about equivalent in size; (3) skin on flanks granular; (4) web extending to base of antepenultimate phalanx of Finger III; (5) dorsum brown, usually with darker transverse markings; (6) venter dull cream with or without small, diffuse, brown spots on chest; (7) narrow pale labial stripe confluent with broad, diagonal subocular mark; narrow, transverse, pale stripe on heels; narrow pale stripe above, and lateral to, cloacal opening; (8) flanks tan with small brown spots.

Osteocephalus planiceps is like *O. leprieurii* in having transverse marks on the dorsum and distinct labial, heel, and supracloacal stripes, but it differs by having dark spots on the flanks, larger and fewer tubercles on the dorsum in males, and smaller size. *Osteocephalus taurinus* is larger, has distinct dark spots or mottling on the venter, and lacks labial, heel, and supracloacal stripes. There is a subtle difference in the color of the iris; in *O. taurinus* it is greenish bronze with heavy black radiating lines, whereas in *O. planiceps* it is coppery bronze with fine radiating black lines. Furthermore, the tibia and head are proportionately longer and the tympanum proportionately larger in *O. planiceps* than in *O. taurinus* (see measurements below and Trueb and Duellman, 1971:Table 2). *Osteocephalus buckleyi* and *O. cabrerai* are smaller, have mixed large and small tubercles on the dorsum in males, areolate flanks, more webbing on the hand, and lack labial, heel, and supracloacal stripes; *O. subtilis* is smaller, has a proportionately smaller tympanum, and broad, transverse marks posteriorly on the dorsum (Martins and Cardoso, 1987). The unnamed, small, bromeliad-breeding species also lacks stripes and spots on the flanks and has more webbing on the hand.

In life, the dorsal ground color varies from dull tan to reddish brown; in 12 individuals, dorsal markings consist of dark olive green to dark brown transverse marks on the head, body, and limbs, whereas four females have a middorsal blotch anteriorly and transverse marks posteriorly, and one subadult female has an indistinct blotch in the scapular region and small dark spots on the rest of the body (Fig. 10). The flanks are dull to creamy tan with small, round dark brown or black spots. The anterior and posterior surfaces of the thighs are brown. The labial, heel, and supracloacal stripes are creamy white, and the venter is white to cream. The iris is coppery bronze with fine black radiating lines. Five of 11 females have small, diffuse grayish brown spots on the chest.

The following measurements and proportions are for three males (the first being the holotype) followed by the range (with mean in parentheses) for eight females: SVL 58.5, 64.6, 65.9, 60.5–85.9 (71.8); tibia length/SVL 0.549, 0.568, 0.539, 0.569–0.676 (0.611); head length/SVL 0.345, 0.351, 0.343, 0.334–0.391 (0.348); head width/SVL 0.320, 0.331, 0.318, 0.315–0.365 (0.327); tympanum/eye 0.816,

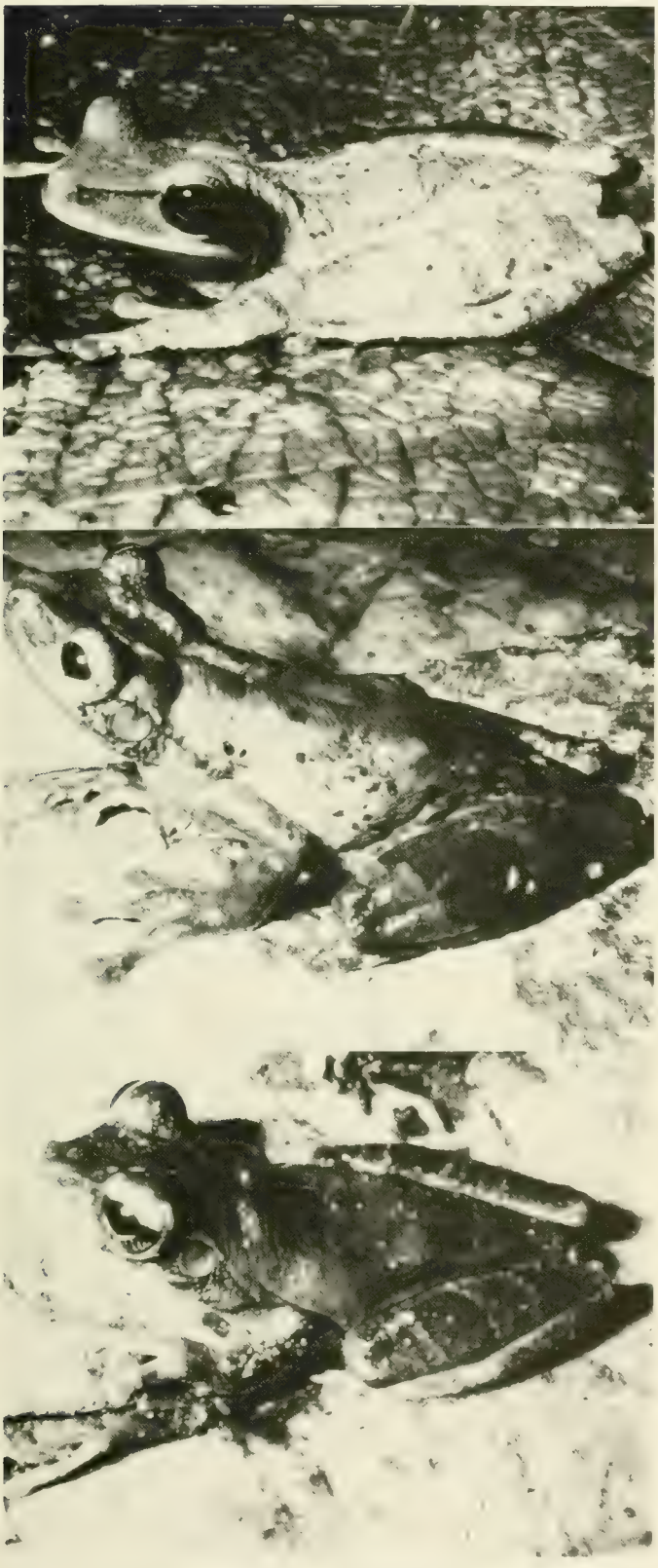


Fig. 10. *Osteocephalus.* Top—*O. planiceps*, KU 221936, adult male, 65.9 mm SVL. Middle—*O. taurinus*, KU 221941, adult female, 90.0 mm SVL. Bottom—*O.* sp., KU 221943, adult male, 43.1 mm SVL.

0.806, 0.885, 0.822–0.901 (0.870). The webbing formula for the outer fingers is **III** (3⁻–3)—(2½–3⁻) **IV**, and the fourth toe has 1½–2 phalanges free of webbing. The holotype and 12 of the 17 new specimens have a bifid distal subarticular tubercle on Finger IV. The four largest females have SVLs of 74.5–85.9 ($\bar{x}$ = 79.7) and masses of 21.4–30.0 ($\bar{x}$ = 25.2); two adult males have SVLs of 64.6–65.9 ($\bar{x}$ = 65.3) and masses of 12.7–15.5 ($\bar{x}$ = 14.1)

Individuals were found at night in the study zones at SJ and NTL and in the floodplain forest at TL; most were on tree trunks or branches 1–5 m above the ground. One female was on a fallen palm stem 0.4 m above the water in the lagoon, and three females were at on bushes at the edge of the lagoon at SJ.

Osteocephalus taurinus Steindachner

This large treefrog is represented by two individuals from the study zone at SJ and three from TL. Two females were on trees 2–2.5 m above the ground at night. Two males were perched on poles in camp at night, and one male was on the ground in camp in open sunlight after a shower.

Three males have SVLs of 66.0–72.7 ($\bar{x}$ = 70.1) and masses of 13.0–21.0 ($\bar{x}$ = 17.0), and two females have SVLs of 75.7 and 90.0, and masses of 28.0 and 43.5, respectively. In measurements and proportions, these specimens fall within the ranges of variation of 59 males and 49 females reported by Trueb and Duellman (1971). All specimens have darkly mottled venters and lack white supracloacal, heel, and labial stripes; three individuals have dark spots on pale flanks, whereas the other two have uniformly dark flanks (Fig. 10). The webbing formula for the outer fingers is **III** (2^{+}–2½)—(2–2^{+}) **IV**; 1.5 phalanges of the fourth toe are free of webbing. The distal subarticular tubercle on the fourth finger is bifid in four specimens.

Osteocephalus species

The existence of a small bromeliad-breeding *Osteocephalus* resembling *O. taurinus* has been recognized in central Amazonia for more than a decade (Zimmerman, 1983; Zimmerman and Bogart, 1984; Hödl, 1990); this species was described as *O. oophagus* from central Amazonas, Brazil by Junger and Schiesari (1995). What was at first thought to be the same species also has been observed at the junction of the Río Yanamono and Río Amazonas and at the Amazon Center for Environmental Education and Research near the junction of Río Sucusari and Río Napo, Loreto, Peru (WED, pers. obs.). The species was heard almost nightly in the study zones at SJ and NTL, as well as in the forest along the stream at TL, but most of the calls originated from high in the trees; one calling male was collected from a terrestrial bromeliad at 2120 h at TL on 17 July.

Having a mass of 4.4, this male has the following measurements: SVL 43.1, tibia length 22.5, head length 16.0, head width 15.4, eye 5.1, tympanum 3.0. The webbing formula for the outer fingers is **III** 2½ —2⁻ **IV**; slightly less than two digits are free of webbing on the fourth toe. The distal subarticular tubercle on the fourth finger is distinctly bifid.

Crests on the lateral margins of the frontoparietals are distinct. Pale stripes are absent on the lips, heels, and above the cloacal opening; darks spots are absent on the flanks, and the venter is immaculate. Coloration in life: dorsum brown with faintly darker brown spots; flanks tan; anterior and posterior surfaces of thighs brown; shanks pale brown with indistinct brown bars; throat and belly cream; ventral surfaces of hind limbs tan; margin of upper lip bronze-tan; iris bronze with radiating black lines and broad, median, horizontal reddish brown streak (Fig. 10); bones white.

The combination of small size and white bones immediately distinguish this species from other *Osteocephalus*. The color of the iris and absence of an axillary membrane distinguish it from *O. cabrerai;* the smooth dorsum and flanks distinguish it from *O. buckleyi,* and the absence of pale stripes on the lips, heels and around the cloacal opening distinguish it from *O. leprieurii* and *O. planiceps*. It differs from *O. oophagus* by having more webbing on the hands and feet, white, instead of green, bones, and a different call. Males characteristically call from water-laden bromeliads; the call is a multiphasic series of notes resembling a laugh. This species, which is known from several localities in Departamento Loreto, Peru, apparently is unnamed.

Phyllomedusa Wagler

The collections contain three of the five species of this genus expected in the region; *P. bicolor* and *P. palliata* were not found. However, a single individual is referred to *P. coelestis,* formerly reported only from the holotype, and one specimen represents a new species in the *Phyllomedusa buckleyi* group, formerly unrecorded from the Amazon Basin.

Phyllomedusa coelestis (Cope)

An adult male (KU 221944) obtained at NTL on 20 July 1993 by Alfonso Miranda and Joseph R. Mendelson III apparently is the first specimen recorded since Cope's (1874) description of the species, which was based on a single male from Moyobamba, Peru. The new specimen was compared with the holotype (ANSP 11384). Because this species has not been identified formerly in the Amazonian anuran fauna, a full diagnosis and description are provided.

Diagnosis.—A member of the genus *Phyllomedusa* (*sensu stricto,* Cruz 1990) defined by the following combination of characters (numbered characters follow Duellman, 1974): (1) snout truncate above, inclined anteroventrally in profile; (2) parotoid glands diffuse or elevated, rounded, not protruding dorsolaterally, extending to midlength of body; (3) dorsal skin shagreen with or without tubercles on limbs; osteoderms absent; (4) first finger shorter than, and opposable to, second; (5) first toe longer than, and opposable to, second; (6) discs on fingers small; (7) forearm much more robust than upper arm; (8) calcar absent; (9) cloacal opening directed posteroventrally at midlevel of thighs; (10) dorsal surfaces and side of head green; (11) flanks green with creamy white, vertical ellipsoids; (12) anterior and posterior surfaces of thighs colored like flanks; (13) throat and chest grayish brown; belly pale orange; (14) ulnar, tarsal, supracloacal stripes and margins of upper eyelid and lower jaw creamy white; (15) iris black with coppery reticulations; (16) palpebrum clear; (17) SVL GG 53.3–64.8.

Of the other 10 nominal species of *Phyllomedusa* in the Amazon Basin, five species differ from *P. coelestis* by having a cream or white iris; of these, *P. atelopoides* is a smaller, brown, terrestrial species, *P. hulli* is a smaller species lacking parotoid glands and markings on the flanks and limbs, *P. tomopterna* has calcars and bright orange-yellow flanks and hidden surfaces of the limbs with vertical brown or lavender bars, *P. vaillanti* has elevated, angular parotoid glands extending to the sacrum and a longitudinal row of white granules along the angle of the gland, and *P. bicolor* is much larger with parotoid glands elevated dorsolaterally and small creamy white spots bordered by black on the flanks and anterior and posterior surfaces of the thighs. *Phyllomedusa boliviana* and an unnamed species resembling *P. boliviana* have a pale labial stripe extending onto the flank, a faintly reticulated venter, and black iris with gold or coppery reticulations (iris black in unnamed species). In *P. palliata* the venter and flanks are cream with brown flecks and the iris is bronze with fine black reticulations; the iris is similarly colored in *P. hypocondrialis,* which has the flanks and hidden surfaces of the thighs orange with black bars and the venter white with black flecks on the chest. *Phyllomedusa tarsius* is most like *P. coelestis,* but in *P. tarsius* males are much larger (SVL 81–90, $\bar{x}$ = 84.1, n = 20), the pattern on the flanks consists of small, irregular pale marks, and males lack vocal slits..

Description.—n = 2 ♂♂ (data for holotype, if different, in parentheses). Body robust; head about as wide as long; snout moderately short, nearly truncate in dorsal view, rounded above and slightly inclined anteroventrally in profile; nostrils protuberant, directed laterally, at level of anterior margin of lower lip; internarial region slightly depressed; canthus rostralis straight, rounded and slightly elevated in section; loreal region barely concave; lips rounded, not flared; top of head flat, slightly depressed below level of canthi; interorbital distance greater than width of upper eyelid; eye large, protuberant; pupil vertically elliptical; palpebrum clear; parotoid gland distinct, elevated, rounded in section, extending from upper eyelid to about midlength of body (diffuse), followed posteriorly by four large, round pustules (absent); supratympanic fold absent; tympanum distinct, round, separated from eye by distance about one half diameter of tympanum.

Axillary membrane absent; upper arm slender; forearm moderately robust; row of low tubercles on ventrolateral edge of forearm from elbow to wrist; fingers long, lacking webbing and lateral fringes; discs small, round; disc on Finger III about one half size of tympanum; relative lengths of fingers I < II < IV < III; first finger opposable to second; subarticular tubercles large, round, elevated; supernumerary tubercles present only on proximal segments of Fingers II–IV, nearly equal in size and shape to subarticular tubercles; palmar tubercle diffuse, barely elevated; thenar tubercle large, elliptical, elevated, bearing pigmented, but not keratinous, nuptial excrescence on inner and dorsal surfaces (Fig. 11).

Hind limb slender; calcar and tubercles on heel absent; transverse dermal fold on heel continuous with row of tubercles on outer edge of tarsus; inner tarsal fold absent; row of low tubercles on ventral surface of tarsus; outer metatarsal tubercle absent; inner metatarsal tubercle small, ovoid, not visible from above; toes long, lacking webbing and lateral fringes; discs round, slightly smaller than those on fingers; relative lengths of toes II < I < III < V < IV;

Fig. 11. Hand and foot of *Phyllomedusa coelestis,* KU 221944. Scale bar = 1 mm.

first toe opposable to second; subarticular tubercles large, round; supernumerary tubercles present only on proximal segments, large, nearly equal to subarticular tubercles (Fig. 11).

Cloacal opening directed posteroventrally at midlevel of thighs; cloacal sheath short, unmodified; clusters of para-anal tubercles absent. Skin on dorsal surfaces of head, body, and limbs shagreen with round tubercles on thighs and shanks (small on thighs, absent on shanks); skin on flanks areolate with (without) scattered low tubercles; skin on throat, chest, belly, and ventral surfaces of forearms and thighs coarsely granular; other surfaces smooth; osteoderms absent; row of low, white tubercles on ventral surfaces of thighs —5 on right, 4 on left (4 on each); proximal tubercle on each thigh much larger than others (2nd on right largest); row of low, white tubercles on ventral surfaces of tarsi—4 on right, 2 on left (indistinct). Tongue broadly lanceolate, shallowly notched posteriorly, free behind for about 40% of its length. Dentigerous processes of vomers bearing teeth—5 on right, 4 on left (4–4), angled posteromedially, located between moderately large, rectangular choanae, moderately separated medially. Vocal sac single, median, subgular; vocal slits short, extending anteromedially from angle of jaw.

Color in preservative: Dorsum dull blue, parotoid glands darkest (no distinction); seven creamy white, vertical ellipsoids (irregularly quadrangular) on each flank; creamy white, vertical ellipsoids (irregular marks) on hidden surfaces of limbs—2 (1) on upper arms, 4 each on forearms (distal ones coalesced) and tarsi, 5 each on anterior (4 with distal ones coalesced) and posterior surfaces of thighs and inner and outer surfaces of shanks; dorsal surfaces of Fingers III and IV and Toes III–V dull blue, of Fingers I and II and Toes I and II cream with brownish blue transverse marks; discs on Fingers I and II and on Toes I–III primarily cream, on Fingers III and IV and on Toes IV and V primarily dark blue. Throat and chest dark brown with small white spot medially on throat (absent) and large white spot (two spots) medially on chest; belly creamy-white laterally, brownish gray anteriorly—with three small white spots medially (absent), dull orange (cream) posteriorly; ventral surfaces of arms and hands cream, with gray suffusion on fingers; ventral surfaces of thighs cream anteriorly and gray posteriorly, of tarsi and feet gray. Creamy white stripes on margin of upper eyelid and on margin of lower jaw extending posteriorly to, or nearly to, first ellipsoid on flank (continuous with first vertical mark); transverse creamy white stripes above cloacal opening and on heels; creamy tan stripes on ventrolateral edges of forearms and tarsi.

Color in life: Dorsum green with pale creamy white ellipsoids on flanks and hidden surfaces of limbs; throat and chest dark grayish brown; belly pale, dull orange; iris black with coppery reticulations (Fig. 12).

Measurements: SVL 64.8 (53.3) , tibia length 31.4 (25.5), foot length 22.6 (17.8), head length, 23.0 (18.2), head width 22.8 (17.6), interorbital distance 8.4 (6.7), internarial distance 5.1 (4.7), eyelid width 6.4 (5.3) , eye-nostril 6.1 (4.8), eye 6.9 (5.3), tympanum 4.0 (3.5).

Remarks.—The holotype is in reasonably good condition although it is soft, and the skin is loose. Most of the discrepancies between the holotype and the new specimen are in dermal characters (pustularity and parotoid glands), the distinctness of which can be due to preservation. However, Cope (1974:121) stated: "... no trace of parotid gland or line of crypts." The distinctness of the parotoid glands is variable in some species of *Phyllomedusa;* as noted by Duellman (1974) in some specimens of *P. tarsius* the glands are diffuse and barely noticeable, whereas in others that are distinct and elevated.

Cope's (1874:121) description of coloration—"Superior surfaces blue, sides yellow, with vertical purple bars. Concealed surfaces light maroon, with yellow spots; on the posterior face of the femur in two series. Belly and throat sea-green, unspotted. Lower lip yellow bordered; upper lip without markings. Upper eyelids yellow bordered."—is at some variance with the holotype and with the new specimen. A pair of distinct white spots are present on the chest. The

Fig. 12. *Phyllomedusa coelestis,* KU 221944, adult male, 64.8 mm SVL.

"sea-green" ventral coloration has been observed in some *P. vaillanti*, but in the new specimen, the throat and chest were brownish gray, and the belly was dull orange. Evidently the stripes and spots that were creamy white in the new specimen and are now white in the holotype were yellow in the holotype when Cope examined the specimen. Cope's "vertical purple bars" are the interspaces (continuous with the dorsal coloration) between the vertical pale marks on the flanks.

The new specimen, having a mass of 13.0, was perched on the limb of a tree 3 m above ground in the study zone NTL at night (2025 hr). Other species of *Phyllomedusa* found at the same locality are *P. hulli, tarsius, tomopterna*, and *vaillanti*. The type locality of *P. coelestis* is Moyobamba, 830 m, at the base of the Andes about 465 km SSW of TL.

Cochran and Goin (1970) reported a specimen (MLS 62, sex unknown, SVL 62.6 mm) from La Providencia, Departamento Caquetá, Colombia, that they referred to *P. boliviana* Boulenger. Photographs of this specimen (Cochran and Goin, Pl. 40) show a lateral color pattern like that of *P. coelestis*. It is likely that this specimen represents a third locality for *P. coelestis* rather than an Amazonian record for *P. boliviana*, which otherwise has been reported only from semiarid regions of Bolivia, Paraguay, and northern Argentina.

Phyllomedusa hulli new species

Holotype.—URP-WED 60198, an adult male, from forest pond at 1.5 km N Teniente López, Provincia Loreto, Departamento Loreto, Peru (02°35'38.9"S, 76°07'02.0"W, 310 m), obtained on 19 July 1993 by Joseph R. Mendelson III and Alfonso Miranda.

Diagnosis.—A member of the *Phyllomedusa buckleyi* group as defined by Cannatella (1980) with the following combination of characters: (1) foot webbing **II** 2^+—3.5 **IV** 3^+—2 **V**; (2) calcar absent; snout sloping in profile; (4) para-anal tubercles present; (5) outer metatarsal tubercle absent; (6) white dorsal pustules present; (7) quadratojugal present; (8) sacro-coccygeal articulation bicondylar.

In comparison with other members of the *Phyllomedusa buckleyi* group (Cannatella, 1980, plus *P. danieli* provisionally placed in the group by Ruíz-Carranza et al, 1988), *P. hulli* is unique in having coarsely granular skin on the dorsum. The dorsal skin is finely granular in *P. buckleyi* and *P. medinai* (smooth in the other species); the former has a smaller tympanum (tympanum/eye = 0.329–0.375, $\bar{x}$ = 0.352, n = 10) that is barely evident, whereas the larger tympanum (tympanum/eye = 0.489) is distinct in *P. hulli*. Furthermore, *P. buckleyi* differs from *P. hulli* by having small calcar and usually having a small outer metatarsal tubercle; *P. psilopygion* has a large calcar, no para-anal tubercles, and a truncate snout (also truncate in *P. lemur*). *Phyllomedusa danieli* is a doubtful member of the group because of its large size (80 mm), toes basally webbed, and yellow iris; the other species have a white iris, toes about one-fourth to one-third webbed, and maximum snout-vent lengths in males of 34.7–44.5.

Description.—n = 1. Head barely wider than body; snout short, narrowly rounded in dorsal view, sloping anteriorly from level of nostrils to margin of lip in profile; nostrils moderately protuberant, directed dorsolaterally, at level posterior to anterior margin of lower jaw; internarial region slightly depressed; canthus rostralis straight, acutely rounded in section; loreal region slightly concave; lips thin, not flared; top of head flat; interorbital distance greater than width of upper eyelid; eyes large, protuberant; pupil vertically elliptical; palpebrum clear; parotoid glands not differentiated; supratympanic fold thin, extending to point above angle of jaw, not obscuring upper edge of tympanum; tympanum round, distinct with slightly elevated annulus, separated from eye by distance equal to two thirds diameter of tympanum.

Axillary membrane absent; upper arm slender; forearm moderately robust; dermal fold from elbow to base of disc on Finger IV narrow, slightly crenulate; fingers moderately short, flattened in section, lacking webbing but having narrow lateral fringe on each side of each digit; discs round; diameter of disc on Finger III equal to diameter of tympanum; relative lengths of fingers I < II < IV < III; distal subarticular tubercles conical; proximal subarticular tubercles round, barely elevated; supernumerary tubercles diffuse, present only on proximal segments of digits; palmar tubercle diffuse; thenar tubercle elliptical, poorly differentiated; thin, keratinous nuptial excrescence on dorsal surface of basal part of thumb (Fig. 13).

Hind limb slender, long; calcar and tubercles on heel absent; outer tarsal fold distinct, crenulate, extending from heel to base of disc on Toe V; inner tarsal fold absent; outer metatarsal tubercle absent; inner metatarsal tubercle low, elliptical, visible from above; toes moderately long with distinct lateral fringes, about one-fourth webbed; webbing formula **III** 2^+—3.5 **IV** 3^+—2 **V**; relative lengths of toes I < II < III < V < IV; discs round, about equal in size to those on fingers; distal subarticular tubercles conical; proximal subarticular tubercles round, elevated; supernumerary tubercles indistinct (Fig. 13).

Fig. 13. Hand and foot of *Phyllomedusa hulli*, URP-WED 60198. Scale bar = 1 mm.

Cloacal opening directed ventrally at lower level of thighs; cloacal sheath long; para-anal tubercles present. Skin on dorsal surfaces, except upper arms and digits coarsely granular; skin on belly weakly granular; skin on other surfaces smooth; one white, elevated wart on body; osteoderms absent. Tongue lanceolate, nearly three times as long as wide, distinctly notched posteriorly, free behind for about one half of its length. Dentigerous processes of vomers each bearing three teeth, angled posteromedially between large reniform choanae, moderately separated medially. Vocal sac single, median, subgular; vocal slit extending from midlateral base of tongue nearly to angle of jaw.

Color in preservative: Head and dorsum of body, limbs (except upper arms), and proximal parts of Finger IV and Toes IV and V dark, dull blue with scattered pale blue flecks; upper arms, flanks, belly, and other surfaces of limbs and digits cream; throat, margin of upper lip, ulnar and tarsal stripes, para-anal tubercles, and lower edge of cloacal sheath white.

Color in life: At night dorsum dark green with small, pale green flecks. By day dorsum pale green; flanks and hidden surfaces of limbs orange; chin, belly, and labial, ulnar, tarsal, and infracloacal stripes white; iris cream (Pl. 1).

Measurements: SVL 37.1, tibia length 18.6, foot length 13.5, head length 24.0, head width 14.1, interorbital distance 5.2, internarial distance 3.0, eyelid width 4.2, eye-nostril 3.9, eye 4.5, tympanum 2.2; mass 1.5 g.

Etymology.—The specific name is a patronym for Dr. Clark Hull, Environmental Manager, Occidental Petroleum Company of Peru; his broad outlook on environmental issues sets an outstanding example.

Remarks.—The holotype was perched on a leaf of a vine 4 m above the ground; the vine was attached to a tree at the edge of the forest pond NTL . The frog was collected at 2225 hr. This pond was visited nightly for nine nights (16–24 July); no other individuals were observed nor was any unknown phyllomedusine call heard. During this time four male *Phyllomedusa tarsius* were found in trees near the pond and four species of *Hyla* (*H. koechlini, parviceps, rhodopepla, sarayacuensis*) were calling from bushes and low herbs in, and around, the pond.

This is the only species of the *Phyllomedusa buckleyi* group known from the Amazon Basin. The other species are mostly confined to cooler montane forests, but *P. buckleyi* ranges from 400–1870 m on the Amazonian slopes of the Andes in Ecuador, and *P. psilopygion* occurs at elevations of 100–300 m on the Pacific lowlands of Colombia (Cannatella, 1980).

Phyllomedusa tarsius (Cope)

Five adult males having well-developed, dark brown nuptial excrescences have SVLs of 82.2–88.7 ($\bar{x}$ = 85.6) and masses of 20.0–30.0 ($\bar{x}$ = 27.4). The parotoid glands are diffuse in three individuals and elevated, round, and extending to midlength of the body in two individuals. One was perched on a tree limb 1.5 m above the ground at night in the study zone at SJ. Four were on limbs of trees 1.5–4.0 m above the ground near the forest pond NTL.

Phyllomedusa tomopterna Cope

One adult male with well-developed nuptial excrescences and having a SVL of 45.0 and mass of 3.5 was in a bush at the edge of the forest clearing at SJ at night. Of two individuals from the study zone NTL, one gravid female having a SVL of 56.6 and mass of 9.5 was on a palm frond 1.2 m above the ground at night on 24 July; the other individual, a juvenile having a SVL of 28.4 and mass of 0.9 was on a leaf 1.5 m above the ground at night on 17 July.

Phyllomedusa vaillanti Boulenger

With the exception of one adult male having a SVL of 59.9 and a mass of 9.6 found on a leaf 1.2 m above the ground at night at NTL, all adults are from SJ, where most were found adjacent to the lagoon at the edge of the study zone. Three small males (SVL = 48.4, 48.8, 49.4; mass = 3.1, 5.6, 5.0) with weakly developed nuptial excrescenses were calling from bushes and trees 0.5–1.5 m above the edge of the water on the night of 5 July. A large adult male (SVL = 53.3, mass = 8.0 g) was on a bush at the edge of the lagoon on 8 July. Only two females were found; a gravid individual having a SVL of 81.5 and a mass of 31.0 was walking on the ground near the lagoon on 2 July. A small female (SVL = 48.2, mass = 4.8 g) containing small ovarian eggs was in a bush about 200 m from the lagoon on 10 July. A juvenile having a SVL of 35.0 and a weight of 1.7 gm also was found on 10 July.

Many metamorphosing and recently metamorphosed young were observed on the ground and on vegetation up to 3 m above the ground near the lagoon at SJ on the nights of 30 June–5 July; 14 individuals with partial tails have SVLs of 20.3–23.6 ($\bar{x}$ = 21.6), tail lengths of 1.2–16.6 ($\bar{x}$ = 7.1), and masses of 0.8–1.7 ($\bar{x}$ = 1.3), whereas nine individuals without tails obtained on 10 July have SVLs of 22.8–26.3 ($\bar{x}$ = 24.5). Ten recently metamorphosed young found at the oxbow lake at TL on 16–23 July have SVLs of 28.2–37.7 ($\bar{x}$ = 30.1) and weights of 1.0–2.7 ($\bar{x}$ = 1.4). Even the smallest of these have the distinctive dorsolateral row of tubercles, which in small individuals are rusty orange instead of white, as they are in larger individuals. In the metamorphosing young the dorsum is dark green, the venter grayish white with pale green spots on the chest, and the iris silver.

The presence of small calling males, large calling males, a gravid adult female, a subadult male and female, and young of various sizes suggest a long reproductive season in this species.

Scinax cruentomma (Duellman)

Of four individuals from TL, one adult male (SVL 23.0, mass 0.3) was on emergent vegetation in a temporary pond at night, one gravid female (SVL 27.7, mass 1.0) was on a leaf 0.5 m above ground in the flood plain forest at night, one subadult male (SVL 19.9, mass 0.2) was on a leaf 2 m above the edge of the oxbow lake at night, and one subadult female (SVL 23.0, mass 0.7) was under a board in a clearing by day. In life, the adults were green with darker green stripes, and the posterior surfaces of the thighs were dark brown; the venter was creamy white, and the iris was bronze with a horizontal red streak.

Scinax funerea (Cope)

Two gravid females having SVLs of 39.9 and 37.6 and masses of 3.4 and 3.8 were perched on branches 5 and 3 m above the ground at night in the study zone at SJ and in the flood plain forest at TL, respectively. At night at the forest pond NTL a spent female having a SVL of 37.7 and a mass of 2.5 was observed running up the trunk of a sapling. Color notes on gravid females in life are: KU 221960—Dorsum pale olive green with dark olive green markings; flanks creamy yellow with black markings; iris coppery bronze. KU 221961—Dorsum mottled reddish brown and dark brown; flanks yellow with dark brown spots; anterior and posterior surfaces of thighs dark brown with pale green streaks; throat and belly dirty cream; ventral surfaces of limbs pale green; iris bronze.

Scinax garbei (Miranda-Ribeiro)

Males were calling from vines and leaves of bushes at the edge of the lagoon at SJ on 1–5 July; some called from a horizontal position, and others were head down. Seven males have SVLs of 32.8–34.9 ($\bar{x}$ = 33.7) and masses of 1.4–2.0 ($\bar{x}$ = 1.76). A single female from the same lagoon has a SVL of 38.5 and a mass of 2.6. The bars on the limbs are pale orange in life, and the snout has a pronounced tubercle; in these characters they are like specimens from Santa Cecilia, Ecuador, but they are slightly smaller (Duellman, 1978). They are quite different from specimens from the junction of the Río Yanamono and Río Amazonas, Loreto, Peru, which have less tuberculate skin, no prominent tubercle on the snout, and red bars on the limbs (Duellman and Wiens, 1993). Furthermore, these specimens (KU 220342–45, 220432–33) are larger; 3 males have SVLs of 34.9–39.2 ($\bar{x}$ = 37.2) and three females have SVLs of 45.0–49.1 ($\bar{x}$ = 46.7).

Scinax rubra (Laurenti)

This species was abundant in clearings at the camps at SJ and TL; individuals were found by day under cover and at night on buildings and in grassy areas, where males called from sticks and vegetation above shallow water. One male with a mass of 1.6 g in grass at night had a dragonfly in its mouth. One gravid female was at the edge of the oxbow lake at TL at night. Thirteen adult males have SVLs of 25.4–35.0 ($\bar{x}$ = 30.3) and masses of 1.3–1.8 ($\bar{x}$ = 1.56); eight gravid females have SVLs of 34.5–40.7 ($\bar{x}$ = 37.9) and masses of 2.1–3.3 ($\bar{x}$ = 2.8).

Duellman and Wiens (1993:39) noted "... specimens from the lower Río Pastaza drainage, Ecuador, are smaller than 'typical' *S. rubra* in the upper Amazon Basin. Also, some specimens from the western edge of the Amazon Basin in Departamento San Martín [Peru] are larger, lack dorsolateral stripes, and have diffuse yellow spots on the posterior surfaces of the thighs." The specimens from SJ and TL are variable in size and color pattern. The range and mean in SVL of these specimens is greater than in a series of 17 males from Santa Cecilia, Ecuador—29.4–33.8 ($\bar{x}$ = 32.1); all of these specimens have dorsolateral stripes. Only 12 (52%) of the specimens from SJ and TL have dorsolateral stripes. The dorsum in the others is olive brown to brown with tan to pale gray mottling. The yellow spots on the posterior surfaces of the thighs are diffuse in nine specimens, four of which have dorsolateral stripes. Thus, the specimens from SJ and TL have combinations of features, individual ones of which are characteristic of populations of *S. rubra* to the north, west, and southwest.

LEPTODACTYLIDAE

Adelophryne

The genus *Adelophryne* was proposed by Hoogmoed and Lescure (1984) for two new species of minute leptodactylid frogs having flattened digits, asymmetrically pointed discs with lateral grooves on the toes, fourth finger reduced in size with only two or three phalanges and one subarticular tubercle. Three additional species were named from northeastern Brazil by Hoogmoed et al. (1994). The present specimens, which exhibit greater digital reduction and have only three functional digits on the hand and foot, obviously represent an undescribed species that is tentatively placed in *Adelophryne*. For ease of comparison, the following diagnosis and description follow the format of Hoogmoed and Lescure (1984).

Adelophryne tridactyla new species

Holotype.—URP-WED 59953, an adult male, from San Jacinto, 190 m, Departamento Loreto, Peru, obtained on 7 July 1993 by Richard A. Leschen.

Referred specimen.—KU 221992, an adult female, from 1.5 km N Teniente López, (02°35'39.0"S, 76°06'59.0"W, 340 m), Provincia Loreto, Departamento Loreto, Peru, obtained on 17 July 1993 by Joseph R. Mendelson III.

Diagnosis.—A minute frog (maximum SVL 12.4) with Finger I not evident externally, Fingers II and IV greatly reduced; Toe I not evident externally, Toe II reduced to tubercle; Toes III and IV greatly reduced; tips of digits asymmetrically pointed; skin on dorsum finely shagreen, flanks and belly black with cream spots.

Adelophryne tridactyla differs from its congeners by having only three externally visible digits on the hand and foot, presence of elliptical tubercle on proximal outer edge of tarsus and lateral fringes on toes, proportionately larger tympanum, and in coloration. *Adelophryne adiastola, barturitensis,* and *gutturosa* lack pale spots on the flanks, whereas *A. pachydactyla* has white flecks on the dorsum and *A. maranguapensis* has a dark hourglass-shaped or X-shaped mark on the dorsum.

Description.—n = 1 ♀, 1 ♂, SVL to 12.4 mm; head slightly wider than long, not as wide as body. Snout long; eye-nostril distance less than diameter of eye; snout bluntly rounded in dorsal view, rounded above and inclined posteroventrally in profile; canthus rostralis indistinct, straight, curved in section; loreal region flat,

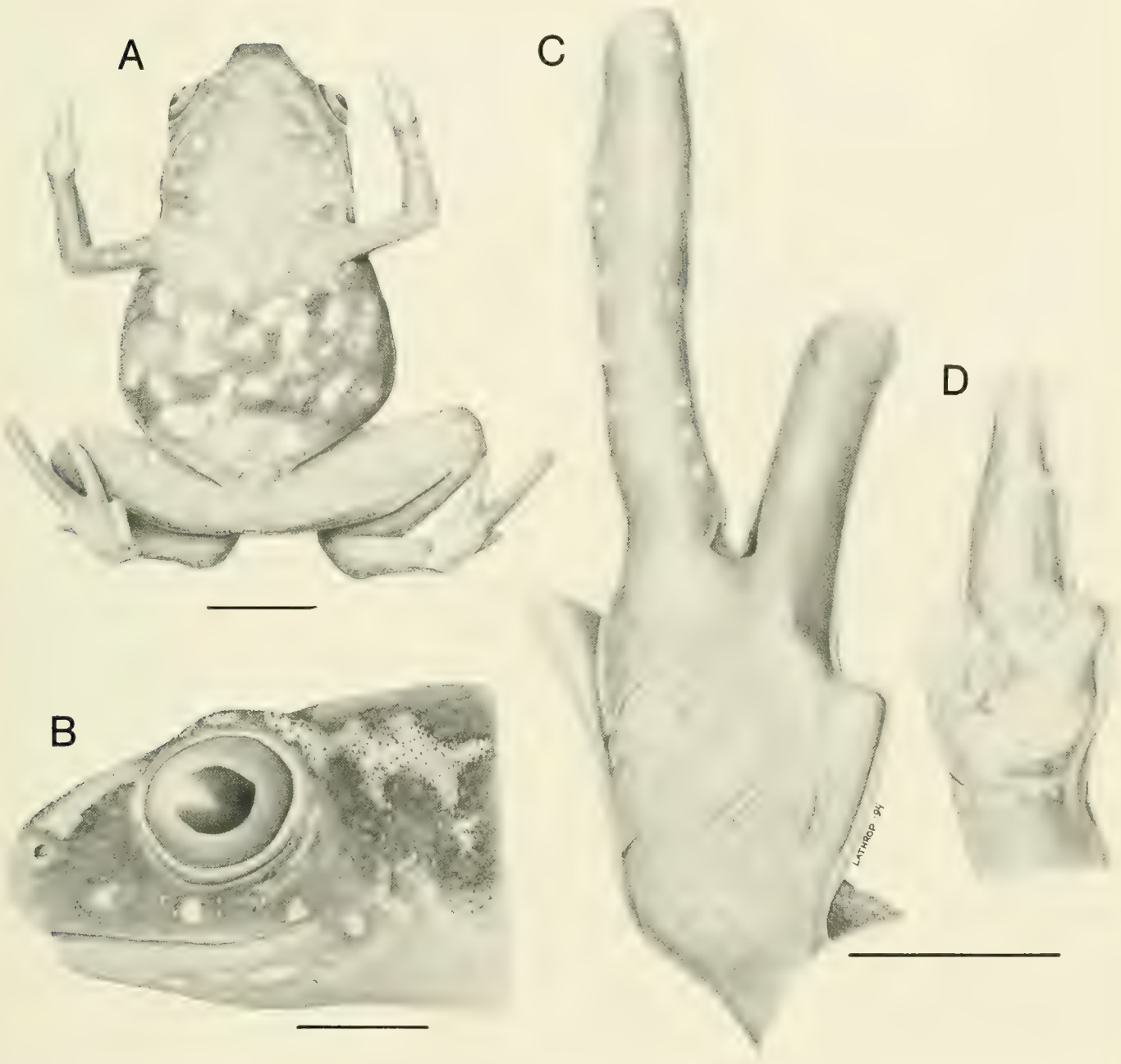


Fig. 14. *Adelophryne tridactyla*, KU 221992, adult female, 11.5 mm SVL. A. Venter. B. Side of head. C. Plantar view of foot. D. Palmar view of hand. Scale bars: A = 2 mm; B–D = 1 mm.

in continuous plane with lips. Nostrils below level of canthus, not protuberant, directed laterally at level of anterior margin of lower jaw; internarial area not depressed. Top of head slightly convex; interorbital distance more than 1.5X width of upper eyelid; eye large, not greatly protuberant; pupil horizontally elliptical. Temporal region vertical; tympanic annulus distinct except posterodorsally where obscured by diffuse supratympanic fold; diameter of tympanum about two-thirds that of eye, separated from eye by distance about one-third diameter of tympanum (Fig. 14).

Dentigerous processes of vomers each bearing 5 or 6 teeth, straight, barely separated medially, located at level between orbits and well posterior to small, ovoid choanae. Tongue lanceolate, not notched posteriorly, attached only anteriorly. Vocal slits long, extending anteromedially from angle of jaw.

Skin on dorsum finely shagreen; that on flanks and venter smooth; discoidal fold absent; folds on wrists and heels, and below tympanum absent. Cloacal aperture a puckered opening directed posteriorly at upper level of thighs.

Hand with large, padlike palm composed of diffuse tubercles; two indistinct subarticular tubercles on Finger III; Fingers II and

III equal in length, short, blunt, completely fused with Finger III; Finger I not evident externally. Finger III with lateral fringe, pointed terminally, without disc (Fig. 14). Nuptial excrescences absent. Phalangeal formula 1–1–3–1; terminal phalanges pointed.

Elliptical tubercle on proximal outer edge of tarsus (otherwise, tarsus smooth); inner metatarsal tubercle small, diffuse; outer metatarsal tubercle absent; subarticular tubercles indistinct; basal plantar surface padlike. Tips of toes dilated into small, asymmetrical discs, slightly wider than toes, lacking circumferential grooves; toes depressed, unwebbed, but with lateral fringes; relative lengths of toes II < V < III < IV. Phalangeal formula (viewed in radiographs) 1–1–3–4–2; terminal phalanges pointed (Fig. 14). When hind limbs flexed at right angles to longitudinal plane of body, heels touch but do not overlap; tibia length 41–43% of SVL.

Measurements: Holotype, KU 221992; SVL 12.4, 11.5; tibia length 5.1, 5.0; foot length 4.4, 4.2; head length 3.6, 3.6; head width 4.0, 4.1; interorbital distance 1.6, 1.6; eyelid 0.9, 1.0; internarial distance 1.0, 1.0; eye-nostril 1.2, 1.1; eye diameter 1.6, 1.5; tympanum diameter 1.0, 0.9; eye-tympanum 0.3, 0.3.

Coloration in preservative: Dorsum of head, body, and limbs brown with pale tan spots and flecks; narrow creamy tan canthal stripe extending along outer edge of upper eyelid and continuous with irregular creamy tan dorsolateral stripe, bordered by dark brown, extending from posterior edge of eyelid to groin; flanks and belly dark brown with large bluish white spots (Fig. 8); upper lip, throat, ventral surfaces of limbs, and anterior and posterior surfaces of thighs brown with cream flecks.

Coloration in life: KU 221992—Dorsum of head, body, and limbs dark brown with cream flecks and narrow cream canthal and dorsolateral stripes; flanks and belly black with cream spots; throat and ventral surfaces of limbs brown with cream flecks; anterior and posterior surfaces of upper arm orange-tan; iris red (Pl. 1).

Etymology.—The specific epithet is an adjective derived from the Greek *daktylos* meaning finger or toe and the Greek prefix *tri-* meaning three; the name refers to the presence of only three functional digits on the hand and foot.

Ecology.—Both individuals were in primary forest. The holotype was in a pan of preservative below an insect-flight intercept trap early in the morning, and the other individual was in a pitfall trap at 2225 h. Both specimens have small ants in their stomachs.

Remarks.—Six specimens (MPEG 5304–05, 5637; RMNH 26812–14) from Tabatinga, Estado Amazonas, Brazil, are like *A. tridactyla* in having reduced digits on the hands and feet. Pending further study, these specimens are tentatively referred to *A. tridactyla*. Tabatinga is about 700 km ESE of San Jacinto.

Comparison of the two specimens of *A. tridactyla* with two of *A. adiastola* (KU 220475, 220564) from Quebrada Vásquez, north side of lower Río Tahuayo, Departamento Loreto, Peru (first Peruvian record) reveals that the latter are slightly larger (SVL 14.1, 14.4), have more granular skin on the dorsum, which is nearly uniform dark brown with no pale canthal and dorsolateral stripe, and hands and feet as described for the type series of *A. adiastola* by Hoogmoed and Lescure (1984).

Examination of radiographs of the type series of *A. tridactyla* and the two specimens of *A. adiastola* showed the phalangeal reduction described in *A. tridactyla* and the phalangeal formula in *A. adiastola* to be 2–2–3–2 in the hand and 2–2–3–4–2 in the foot. Thus, these two specimens of *A. adiastola* have phalangeal reduction in the foot, as compared with the type series, in which the phalangeal formula is 2–2–3–4–3 (Hoogmoed and Lescure, 1984). According to Hoogmoed et al. (1994), the phalangeal formulae for the hands of *A. barturitensis* and *A. maranguapensis* are 2–2–3–3, whereas that of *A. pachydactyla* is like that of *A. adiastola*. The phalangeal formulae for the feet of the three species in eastern Brazil is 2–2–3–4–3. In comparison with *A. adiastola*, the number of carpals is reduced in *A. tridactyla*, which has one large distal carpal and two (? three) smaller proximal carpals. The great digital reduction in *A. tridactyla* suggests that this species might be placed in a different genus, but until sufficient material is available to make osteological preparations for adequate comparison, the species is placed in *Adelophryne*.

Adenomera hylaedactyla Cope

This small, terrestrial species was common in the study zones at SJ and NTL and in the floodplain forest at TL; nine of 21 specimens were taken in pitfall traps. Ten individuals were found at night; nine were active on the ground by day, and two were beneath cover by day. Six males have SVLs of 18.8–24.1 ($\bar{x}$ = 21.1) and masses of 0.3–1.1 ($\bar{x}$ = 0.72), and 13 females have SVLs of 23.3–27.8 ($\bar{x}$ = 25.1); 10 gravid females have masses of 1.0–1.5 ($\bar{x}$ = 1.17) and two spent females, 0.7 and 1.2. The smallest juvenile has a SVL of 7.2 and a mass of < 0.1. In life, the dorsum varies from pale tan with brown spots to dull gray. The venter is creamy white. Of 21 specimens, 18 have a short, narrow, middorsal stripe posterior to the sacrum; one has a broad cream dorsolateral stripe, and four have dull red, granular dorsolateral stripes.

Heyer (1973; pers. comm.) distinguished *A. hylaedactyla* from *A. andreae* by the shape of the tips of the digits—rounded in section in *A. hylaedactyla* and flattened in *A. andreae*. Examination of specimens from throughout eastern Peru and Ecuador reveals both types of digital discs, but the discs of many individuals are intermediate in structure. The distinction between these two nominal species is not convincing, and the oldest available name is used here.

Ceratophrys cornuta (Linnaeus)

This terrestrial species is represented only by a large skull from TL. The skull (complete except for the premaxillae) has a width of 51.3. Using the statistics for head width and SVL relationships in this species given by Duellman and Lizana (1994), the present specimen must have had a SVL of about 135 mm.

Edalorhina perezi Jiménez de la Espada

Four individuals were collected in pitfall traps (two at SJ and two at NTL). Two adult males have SVLs of 31.6 and 31.7 and masses of 2.6 and 3.7, whereas two juveniles have SVLs of 23.5 and 26.3 and masses of 0.7 and 1.1. These four specimens have Type 2 dorsal skin texture and Type 2 ventral color pattern identified by Duellman and Morales

(1990); these patterns agree with their analysis of geographic variation in that all specimens from the drainages of the Río Pastaza and Río Napo have Type 2 ventral color pattern, whereas 8.9% of specimens from the Río Napo drainage and 54.5% of the specimens from the Río Pastaza drainage have Type 2 dorsal skin texture.

Eleutherodactylus acuminatus Shreve

One male having a SVL of 16.9 was on a leaf of a bush 1 m above ground at the edge of the forest at SJ.

Eleutherodactylus altamazonicus Barbour and Dunn

One subadult female having a SVL of 17.6 and a mass of 0.3 was on the leaf of an herb at night at TL. In life, the groin and hidden surfaces of the thighs were red with black markings.

Eleutherodactylus delius new species

Holotype.—URP-WED 59957, an adult female, from the study zone at San Jacinto, (02°18'44.8"S, 75°51'46.0"W, 183 m), Provincia Loreto, Departamento Loreto, Peru, obtained on 7 July 1993 by Alfonso Miranda.

Diagnosis.—Scheme following Lynch and Duellman (1980) for ease of comparison. A member of the *Eleutherodactylus unistrigatus* group as defined by Lynch and Duellman (1995) with the following combination of characters: (1) skin of dorsum smooth; skin of venter granular; (2) tympanic annulus and tympanic membrane distinct, diameter of annulus 40% diameter of eye, separated from eye by distance equal to diameter of tympanum; (3) snout acutely rounded in dorsal view, round in profile; canthus rostralis angular; (4) upper eyelid 73.7% of interorbital distance, lacking tubercles; cranial crests absent; (5) vomerine odontophores absent; (6) males unknown; (7) first finger shorter than second; toepads large, subtruncate; toepad on Finger III equal to length of tympanum; (8) fingers with lateral keels; (9) ulnar tubercles present; (10) tubercles on heel present; outer edge of tarsus tuberculate; inner edge of tarsus smooth; (11) two metatarsal tubercles; inner elliptical, five times size of round outer tubercle; supernumerary plantar tubercles absent; (12) toes with lateral keels; webbing absent; toepads smaller than those on fingers; Toe V much longer than Toe III; (13) dorsum tan with three longitudinal brown stripes; posterior surfaces of thighs brown; venter cream; (14) adult female 30.9 mm SVL.

Eleutherodactylus delius differs from all other Amazonian members of the genus by lacking vomerine odontophores and having a dorsal pattern consisting of dark brown longitudinal stripes on a tan ground color.

Description.—$n = 1$ ♀. Head not wide as body, longer than wide; head width 39.8% of SVL; head length 42.7% of SVL; snout long, slightly protruding beyond margin of lip, acutely rounded in dorsal view, rounded in profile; eye-nostril distance 12.6% of SVL; upper eyelid lacking tubercles; eyelid width 73.7% of interorbital distance. Top of head flat; cranial crests absent; canthus rostralis straight, angular in section; loreal region noticeably concave; lip slightly flared anterior to orbit; internarial area slightly depressed; nostril protuberant laterally, directed dorsolaterally at point slightly posterior to anterior margin of lower jaw. Supratympanic fold moderate, curving posteroventrally from posterior corner of orbit, obscuring posterodorsal part of tympanic annulus; tympanum round, distinct, separated from eye by distance equal to diameter of tympanic annulus, which is 40.5% of eye diameter. Choanae small, round, not obscured by palatal shelf of maxillary arch; vomerine odontophores absent. Tongue broadly elliptical, barely notched posteriorly, free behind for about 40% of its length.

Skin on dorsum of head, body, and limbs smooth with scattered minute pustules; dermal folds absent on dorsum; skin on flanks weakly granular; belly and ventral surfaces of thighs granular; other ventral surfaces smooth; discoidal fold present; ulnar tubercles low, largest distally; pair of small heel tubercles present; row of low tubercles on outer edge of tarsus. Cloacal opening puckered, directed posteroventrally at upper level of thighs.

Forearm slender; fingers moderately long with broad lateral keels and large, subtruncate discs; disc on Finger I distinctly smaller than those on other fingers; relative lengths of fingers I < II < IV < III; subarticular tubercles large, subconical; supernumerary tubercles absent; palmar tubercle bifid, elevated; thenar tubercle elliptical, elevated. Hind limbs moderately slender; heels broadly overlapping when hind limbs flexed at right angles to axis of body; tibia length 54.4% of SVL; foot length 46.0% of SVL. Thick tarsal fold on distal one third of tarsus; inner metatarsal tubercle large, elliptical; outer metatarsal tubercle small, round; toes moderately long, bearing lateral keels and subtruncate discs noticeably smaller than those on fingers; relative lengths of toes I < II < III < V < IV; Toe III extending to distal edge of penultimate subarticular tubercle on Toe IV; Toe V extending to point slightly distal to distal subarticular tubercle on Toe IV; subarticular tubercles large, subconical; supernumerary tubercles absent.

Color in preservative: Dorsum creamy tan with narrow, black canthal and supratympanic stripes; tympanum black; prominent dark brown bar extending anteroventrally from orbit to margin of upper lip, which otherwise bordered by brown spots. Broad dark brown middorsal (with narrow cream middorsal line) and dorsolateral stripes extending from level of eyelids to posterior end of body; faint, narrower brown paravertebral stripes extending from snout to sacrum; faint brown transverse bars on limbs; 2 bars each on forearm, thigh, shank, and tarsus. Flanks cream with brown flecks anteriorly; anterior and posterior surfaces of thighs pale brown; cloacal region and outer edge of tarsus dark brown; venter cream with minute black flecks on throat, chest, and ventral surfaces of hind limbs.

Color in life: Dorsum yellowish tan with pale brown stripes on body and transverse bars on limbs; infracanthal region dark brown; tympanum and supratympanic and suborbital bar black; posterior surfaces of thighs brown; ventral surfaces of limbs lavender; belly creamy white; throat pale tan with cream spots; iris gold with median horizontal reddish brown streak (Pl. 1).

Measurements: SVL 30.9, tibia length 16.8, foot length 14.2, head width 12.3, head length 13.2, interorbital distance 3.8, upper eyelid width 2.8, eye-nostril 3.9, eye diameter 3.7, tympanum diameter 1.5, eye-tympanum 1.5.

Ecology.—The only known specimen, a gravid female with a mass of 2.1 was on leaf litter in primary forest at 0635 h.

Etymology.—The specific name is a noun in apposition and a patronym for Carlos Delius, President of Occidental Petroleum Company of Peru. His name is associated with this distinctive species in grateful appreciation for the ex-

tensive logistic support provided by his company.

Remarks.—The description of a new species of *Eleutherodactylus* based on a single specimen would be unthinkable to many herpetologists. However, this specimen is so distinctively different from any other Amazonian species that it is inconceivable that it is a variant of a known species.

Eleutherodactylus diadematus (Jiménez de la Espada)

This species was found in the study zones at SJ and NTL and in the floodplain forest at TL. Four were on vegetation 0.3–2.0 m above ground at night; three were on the forest floor—two at night and one by day. One adult male has a SVL of 32.5 and a mass of 1.9; one adult female has a SVL of 40.9 and a mass of 5.0, and a subadult female has a SVL of 31.6 and a mass of 1.2. Four juveniles have SVLs of 17.5–24.7 ($\bar{x}$ = 20.6) and masses of 0.4–1.0 ($\bar{x}$ = 0.65). All specimens have dark diagonal bars on the flanks. In life the dorsal ground color varies from dark brown to tan, and there seems to be ontogenetic change in coloration. For example, the coloration of a juvenile having a SVL of 17.5 was: Dorsum brown; heels orange; posterior surfaces of thighs brown; flanks with dark brown and pale green diagonal bars; groin pink; venter white mottled with gray; iris bronze above and gray below. In contrast, an adult female having a SVL of 40.9 mm was: Dorsum tan irregular brown spots; flanks cream with brown diagonal bars; groin and anterior surfaces of thighs black and yellow; posterior surfaces of thighs black; venter cream with dark brown mottling; iris reddish copper.

Eleutherodactylus lanthanites Lynch

In the study zone at SJ, two gravid females having SVLs of 39.3 and 38.9 and masses of 3.0 and 3.3 were on the forest floor at 0630 h, and a subadult female having a SVL of 23.5 and a mass of 0.6 g. was in a pitfall trap at 0700 h. Color notes on the subadult female in life are: Dorsum dark brown; venter creamy yellow; ventral surfaces of limbs orange; posterior surfaces of thighs dark brown; throat laterally orange-tan. In preservative, all specimens have a median cream stripe on a gray throat.

Eleutherodactylus luscombei new species

Holotype.—URP-WED 60412, an adult male from the study zone at 1.5 km N Teniente López, (02°35'39.6"S, 76°06'55.0"W, 312 m), Provincia Loreto, Departamento Loreto, Peru, obtained on 23 July 1993 by David M. Webb.

Referred specimens.—KU 222002, an adult female, from the type locality, KU 222004, an adult male, from the type locality, KU 222006, an adult male from Teniente López, URP-WED 59865 and URP-WED 60040 (juveniles) from San Jacinto, Departamento Loreto, Peru; KU 222003 and URP-WED 60413 (juveniles), KU 222005 (subadult male) from the type locality; URP-WED 60320 and KU 222007 (juveniles), URP-WED 60319 (subadult male) from Teniente López.

Diagnosis.—Scheme following Lynch and Duellman (1980) for ease of comparison. A member of the *Eleutherodactylus unistrigatus* group as defined by Lynch and Duellman (1995) with the following combination of characters: (1) skin of dorsum shagreen with scattered pustules and W- or \/-shaped dermal ridges in scapular region; skin of venter granular; (2) tympanic annulus and membrane distinct, diameter of annulus about one third diameter of eye, separated from eye by distance about equal to diameter of tympanum; (3) snout round in dorsal view and in profile; canthus rostralis acutely rounded; (4) width of upper eyelid 70–92% of interorbital distance; without tubercles; cranial crests absent; (5) vomerine odontophores prominent, dentigerous; males lacking vocal slits, vocal sac, and nuptial excrescences; (7) first finger shorter than second; toepads round; toepad on Finger III slightly smaller than diameter of tympanum; (8) fingers with lateral keels; (9) ulnar tubercles absent; (10) tubercles on heel absent; outer edge of tarsus smooth; inner edge of tarsus with row of low tubercles distally; (11) one metatarsal tubercle; inner tubercle large, elliptical; outer tubercle absent; supernumerary plantar tubercles small, round; (12) toes with lateral keels; webbing basal; toepads about equal in size to those on fingers; Toe V much longer than Toe III; (13) dorsum brown with top of head and snout (or only snout) cream or tan; posterior surfaces of thighs dark brown; venter cream, finely to heavily flecked with black; (14) adults small; 3 males 19.1–19.9 ($\bar{x}$ = 19.5) SVL; 1 female 26.1 SVL.

In the middle and upper Amazon Basin there are 24 known species of the *Eleutherodactylus unistrigatus* group; these are species with granular skin on the venter and expanded toepads (Lynch, 1976). Of these, five (*E. aaptus, bearsei, diadematus, sulcatus,* and *ventrimarmoratus*) are much larger than *E. luscombei;* three others (*E. acuminatus, paululus,* and *pseudoacuminatus*) are green in life. Four species (*E. carvalhoi, croceoinguinis, toftae,* and *variabilis*) differ from *E. luscombei* by having large yellow or orange spots in the groin. Of the remaining species, *E. altamazonicus* and *E. imitatrix* differ by having tuberculate skin on the dorsum, *E martiae* by having dorsolateral folds and a partially concealed tympanum, *E. orphnolaimus* by having tubercles on the eyelids and snout, and *E. quaquaversus* by having calcars and a concealed tympanum. Other species differ mainly in coloration—*E. lacrimosus* by having a pale dorsum with dark markings but no labial bars, *E. lythrodes* by having a black dorsum and black and red venter, *E. zimmermanae* by lacking vomerine odontophores, and *E. delius* by lacking vomerine odontophores and having dark longitudinal stripes on a pale dorsum. The remaining two species are most similar to *E. luscombei; E. ockendeni* is slightly larger and lacks pale coloration on the snout and top of the head, whereas, *E. trachyblepharus* is smaller, has a partially concealed tympanum, lacks lateral keels on the digits and dermal folds on the dorsum (but may have W-shaped dark mark in scapular region), and has two metatarsal tubercles.

Description.—n = 3 ♂♂, 1 ♀. Head as wide as body, longer than wide; head width 38.7–39.8% ($\bar{x}$ = 39.3) of SVL; head length 42.7–47.4% ($\bar{x}$ = 44.9) of SVL; snout moderately long, barely protruding beyond margin of lip, round in dorsal view and in profile; eye-nostril distance 12.6–13.6% ($\bar{x}$ = 13.1) of SVL; upper

eyelid smooth; width of upper eyelid 70.4–91.7% ($\bar{x}$ = 83.0) of interorbital distance. Top of head flat; cranial crests absent; canthus rostralis shallowly curved, acutely rounded in section; loreal region noticeably concave; lip slightly flared anterior to orbit; internarial area barely depressed; nostril slightly protruding, directed laterally at point just behind level of anterior margin of lower jaw. Supratympanic fold diffuse, obscuring posterodorsal part of tympanic annulus; tympanum distinct, separated from eye by distance slightly less than diameter of tympanic membrane, which is 33.3–37.1% ($\bar{x}$ = 35.8) diameter of eye. Choanae small, ovoid, not obscured by palatal shelf of maxillary arch; vomerine odontophores small, prominent, moderately separated medially, each bearing 2 or 3 teeth in males, 5 in female. Tongue cordiform, shallowly notched posteriorly, free behind for about 40% of its length; vocal slits and vocal sac absent.

Skin of dorsum of head, body, and limbs shagreen with W- or \/-shaped dermal folds in scapular region followed posteriorly by pair of tubercles; skin on flanks shagreen; skin on belly and posteroventral surfaces of thighs coarsely granular; other ventral surfaces smooth; discoidal fold barely evident; ulnar tubercles absent; heel tubercles absent; no tubercles on outer edge of tarsus. Cloacal opening puckered, directed posteroventrally at upper level of thighs.

Forearm slender; fingers moderately short, bearing narrow lateral keels and round discs; disc on Finger I smaller than those on other fingers; relative lengths of fingers I < II < IV < III; subarticular tubercles moderately large, round, elevated; supernumerary tubercles small, round, only on proximal segments; palmar tubercle bifid, elevated; thenar tubercle elliptical, slightly elevated; males lacking nuptial excrescences (Fig. 15). Hind limb moderately slender; heels broadly overlapping when hind limbs flexed at right angles to axis of body; tibia length 52.0–57.6% ($\bar{x}$ = 54.9) of SVL; foot length 41.3–48.7% ($\bar{x}$ = 46.1) of SVL. Row of three of four slightly elliptical tubercles on distal third of inner edge of tarsus; inner metatarsal tubercle elliptical; outer metatarsal tubercle absent; toes moderately long, bearing lateral keels and round discs subequal in size to those on Fingers II–IV; relative lengths of toes I < II < III < V < IV; Toe III extending to middle of penultimate subarticular tubercle on Toe IV; Toe V extending to middle of distal subarticular tubercle on Toe IV; basal webbing between all toes except first and second; subarticular tubercles small, round; supernumerary tubercles minute (Fig. 15).

Fig. 15. Hand and foot of *Eleutherodactylus luscombei*, URP-WED 60412. Scale bar = 1 mm.

Color in preservative: Dorsum dark brown with black dermal ridges and scapular tubercles, diffuse dark brown diagonal bar extending posteroventrally from sacrum onto flank, and dark brown bars on limbs—one broad bar on forearm and four narrow bars each on thigh, shank, and tarsus. Flanks brown with diffuse cream flecks; lips barred with dark brown. Anterior and posterior surfaces of thighs dark brown; heels creamy tan in two males; narrow cream supracloacal stripe in three males. Top of head and snout pale tan in KU 222006; only snout tan in KU 222002 and URP-WED 60412; top of head and snout not paler in KU 222004. Venter of body pale cream with brown flecks on throat and chests in males and more dense flecks over entire venter in female. Top of head and snout pale in three of eight juveniles; one juvenile with only snout pale.

Color in life: Dorsum dark brown with black tubercles in scapular region, darker brown transverse bars on limbs, and indistinct diagonal marks on flanks; posterior surfaces of thighs dark brown; venter dusky cream with or without brown flecks; upper lip tan or cream with dark brown bars; iris orange-copper. In those specimens having a pale snout and top of head, this area is creamy tan to pale reddish tan (Pl. 1).

Measurements: One female followed by range (mean in parentheses) of three males: SVL 26.1, 19.1–19.9 (19.5); tibia length 13.7, 10.2–11.4 (10.9); foot length 10.8, 9.2–9.5 (9.3); head length 11.5, 8.5–9.3 (8.8); head width 10.3, 7.5–7.8 (7.7); interorbital distance 3.0, 2.4–2.7 (2.5); eyelid width 2.7, 1.9–2.2 (2.0); eye-nostril distance 3.3, 2.5–2.7 (2.6); eye diameter 3.5, 2.8–3.0 (2.9); tympanum diameter 1.2, 1.0–1.1 (1.03), eye-tympanum distance 1.2, 0.9–1.0 (0.97).

Ecology.—All individuals were on leaves of herbs and bushes 0.1–1.0 m above the ground in primary forest at night.

Etymology.—The specific name is a patronym for B. Anthony (Tony) Luscombe, President, Asociación de Ecología y Conservación, Lima, Peru, in recognition of his many years of persistent efforts to integrate biological inventories and conservation programs in Peru. Not coincidentally, the clearly demarcated coloration of the top of the head of many specimens of this species is parallel to that of Tony Luscombe.

Remarks.—The one gravid female has a mass of 1.3, and three adult males have masses of 0.4–0.6 ($\bar{x}$ = 0.5). The two smallest juveniles have SVLs of 9.0 and 10.4 and masses of < 0.1.

Eleutherodactylus malkini Lynch

One male was on a fallen palm frond 1 m above the ground at night and one juvenile was on the forest floor by

day in the study zone at NTL; all other specimens are from TL, where five were on roots 0.2–0.4 m above the ground at the edge of a stream at night, two were on the forest floor on the floodplain by day, and three were on low vegetation at the edge of the oxbow lake at night. Six adult males have SVLs of 27.5–33.7 ($\bar{x}$ = 32.1) and masses of 2.0–2.5 ($\bar{x}$ = 2.2); three adult females have SVLs of 39.9–47.9 ($\bar{x}$ = 43.6) and masses of 4.9–7.4 ($\bar{x}$ = 6.4). In living adults the dorsum is pale orange tan with small, dark brown spots, and the posterior surfaces of the thighs are black with greenish yellow flecks; the throat is white, and the rest of the venter is yellow. The iris is bronze with a median, horizontal red streak. These specimens match well the description of this species by Lynch (1980) and provide the first description of coloration in life.

Eleutherodactylus martiae Lynch

One female was on a leaf 0.5 m above the ground at night in the study zone at SJ; in the study zone at NTL one male and one female were on the forest floor by day, and one female and two males were on leaves of herbs 0.1–0.7 m above ground at night. Three males have SVLs of 12.7–15.0 ($\bar{x}$ = 13.7) and masses of 0.1–0.3 ($\bar{x}$ = 0.17); one female with minute ovarian eggs has a SVL of 15.9 and a mass of 0.3, whereas two gravid females have SVLs of 20.1 and 21.8 mm and masses of 0.5 and 0.7. Structurally these specimens compare favorably with paratypes from Santa Cecilia, Ecuador, except that vomerine odontophores are not evident in any of the present specimens. Most topotypic specimens have dense dark flecks on the venter, whereas four of the present specimens have only scattered flecks on the venter. In life, the dorsum is dark brown to reddish brown, and the flanks are tan with brown diagonal marks; the posterior surfaces of the thighs are dark brown to black, and the iris is bronze with a median, horizontal red streak. One male had a brown dorsum with pale green streaks and a dark gray venter with creamy white flecks

Eleutherodactylus nigrovittatus Andersson

Six specimens are from the study zone at SJ (2 in pitfall traps by day, 2 on the forest floor by day and 2 by night) and two are from the study zone at NTL (forest floor by day). Four males have SVLs of 15.4–17.5 ($\bar{x}$ = 16.6 and masses of 0.4–0.5 (0.47), and three females (2 gravid) have SVLs of 19.1–20.8 ($\bar{x}$ = 19.8) and masses of 0.6–0.9 ($\bar{x}$ = 0.73). All individuals have a black anal patch and black diagonal mark in the groin; the bars on the limbs are distinct, and in life the forearms are orange. Six individuals have a faint, narrow, middorsal line posterior to the sacrum.

Eleutherodactylus ockendeni (Boulenger)

Individuals were found in the study zones at SJ and NTL and in the floodplain forest at TL. A juvenile that was amid leaf litter by day, and a minute juvenile (SVL 8.7, mass <0.1) in a rotting log at night. One adult male (SVL 18.6, mass 0.5) and three gravid females were on leaves of bushes 0.2–2.0 m above the ground at night. The females have SVLs of 27.7–31.8 ($\bar{x}$ = 29.8) and masses of 1.6–1.7 ($\bar{x}$ = 1.63). In life the dorsum is tan at night and brown by day; the flanks are tan, and the posterior surfaces of the thighs are dark brown.

Eleutherodactylus peruvianus (Melin)

Both adults and juveniles were active on the forest floor by day and perched on low vegetation (up to 0.5 m) at night in the floodplain forest at TL and in the study zone at NTL. At NTL on 22 July, a male with a mass of 1.7 was in amplexus with a female having a mass of 5.8 on the forest floor at 0740 h. Six males have SVLs of 22.3–28.9 ($\bar{x}$ = 26.4) and masses of 0.6–2.0 ($\bar{x}$ = 1.5), and one gravid female has a SVL of 41.4 and a mass of 5.8. The smallest of eight juveniles has a SVL of 6.0 mm and a mass of < 0.1. In life the dorsum varies from uniform dull red to olive tan in small juveniles. In larger juveniles and in adults, the dorsum is reddish tan with brown chevrons extending laterally onto the flanks and crossbars on the limbs; the posterior surfaces of the thighs are dark brown with minute red flecks. The face mask and postorbital stripe are dark brown; the venter is creamy white with or without brown flecks on the chest. The iris is bronze with a median, horizontal red streak. The amplectant pair and one juvenile have a broad creamy white labial stripe that is continuous with the same color on the upper arm. In preservative, adults have a variable intensity of gray mottling on the throat. In one male the mottling is nearly black, and in one male and the adult female the mottling is dark and extends onto the anterior part of the belly.

Eleutherodactylus quaquaversus Lynch

Two subadult females (one from the floodplain forest at TL and one from the study zone at NTL) were on low vegetation at night. These have SVLs of 17.9 and 18.8 and masses of 0.2 and 0.5, respectively. In contrast to adults from Ecuador, the tubercle on the heel is barely evident, but the tubercles on the margin of the upper eyelid are present; furthermore, the venter is more heavily flecked with black than in Ecuadorian specimens. These specimens apparently are the first records from Peru. According to Lynch's (1980) review of Amazonian *Eleutherodactylus*, this species is known from elevations of 320–1830 m in the upper Amazon Basin and on the Amazonian slopes of the Andes in Ecuador; the closest record to the present localities is Cusuime, Provincia Morona-Santiago, Ecuador.

Eleutherodactylus sulcatus (Cope)

Two individuals are from the study zone at NTL. A juvenile having a SVL of 17.1 and a mass of 0.5 was on the forest floor by day. The dorsum was mottled brown and tan with grayish white markings—narrow middorsal line, heels, and diagonal bar below the orbit. The posterior surfaces of the thighs were black with a longitudinal white line; the belly was white with black flecks, and the iris was grayish

bronze with fine black reticulation. An adult female having a SVL of 44.5 and a mass of 10.0 was in a snap trap in the morning; the dorsum was dull tan, and the venter was cream.

Ischnocnema quixensis (Jiménez de la Espada)

Found in the study zones at SJ and NTL and in the floodplain forest at TL, most individuals were taken at night, but five were found by day. Four males have SVLs of 37.2–40.9 ($\bar{x}$ = 38.9) and masses of 2.9–7.0 ($\bar{x}$ = 5.4); nine gravid females have SVLs of 41.2–53.7 ($\bar{x}$ = 48.2) and masses of 4.4–17.0 ($\bar{x}$ = 10.7). The smallest of seven juveniles has a SVL of 16.9 and a mass of 0.2 g.

Leptodactylus pentadactylus (Laurenti)

A nongravid female having a SVL of 148.2 and a mass of 270 was at the side of a road at night at SJ, and two juveniles having SVLs of 61.8 and 66.9 and masses of 19.0 and 27.6 were in pitfall traps at 0650 h near the lagoon at SJ. Two other individuals are from the oxbow lake at TL, and another is from the forest pond at NTL. The first of these is a juvenile having a SVL of 79.7 and a mass of 43.0; the others are a juvenile having SVL of 47.3 and mass of 6.4 g, and a subadult male having a SVL of 102.9 and a mass of 126 g.

Leptodactylus rhodomystax Boulenger

Three juveniles found on the forest floor at night in the study zone at NTL have SVLs of 26.5–39.6 ($\bar{x}$ = 33.6) and masses of 1.3–3.9 ($\bar{x}$ = 2.9). In life, the dorsum and flanks are orange-tan with dark brown spots on the former; the hind limbs are black with cream yellow spots on the hidden surfaces of the thighs. The belly is orange-tan with creamy white spots, and the prominent labial stripe is pinkish white; the iris is dull red.

Leptodactylus wagneri (Peters)

This name is used in the restricted sense of Heyer (1994). Five individuals were at the margins of the forest pond at night at NTL, and one juvenile was at the edge of a small stream by day at NTL. One adult male with thumb spines has a SVL of 56.5 and mass of 18.8, and a subadult male has a SVL of 40.9 and mass of 7.0. One gravid female has a SVL of 77.5 and a mass of 58.0, and a subadult female has a SVL of 65 mm and a mass of 33.8. Two juveniles have SVLs 14.0 and 26.0 and masses of 0.1 and 1.6.

Lithodytes lineatus (Schneider)

Of the two specimens from NTL and 11 from SJ, all were on the forest floor by day or removed from pitfall traps by day, except two juveniles taken at night, one on the forest floor and one sleeping on a dead *Cecropia* leaf 0.1 m above the ground. Three adult males have SVLs of 33.1–37.5 ($\bar{x}$ = 35.9) and masses of 2.9–4.9 ($\bar{x}$ = 3.7); three gravid females have SVLs of 43.8–47.2 ($\bar{x}$ = 45.2) and masses of 3.4–6.2 ($\bar{x}$ = 4.47), and two females with small ovarian eggs have SVLs of 37.7 and 39.8 and masses of 3.1 and 3.2, respectively. The three smallest juveniles have SVLs of 14.9–15.6 ($\bar{x}$ = 15.3) and masses of 0.2–0.4 ($\bar{x}$ = 0.3).

Physalaemus petersi (Jiménez de la Espada)

Of 64 individuals from the study zone at SJ, 52 were in pitfall traps at night or at dawn. On 30 June, three males were calling from the edge of lagoon at SJ, and 18 individuals were removed from pitfall traps within 10 m of the lagoon. One individual was removed from a pitfall trap in the study zone at NTL, and six were found in the floodplain forest at TL. Of all 71 specimens, seven were found on the forest floor by day and five at night; one of the latter was eating termites. Twelve adult males have SVLs of 21.0–24.4 ($\bar{x}$ = 22.5) and masses of 0.7–1.2 ($\bar{x}$ = 0.94); 15 adult females have SVLs of 26.0–30.4 ($\bar{x}$ = 28.7) and masses of 1.4–3.3 ($\bar{x}$ = 1.86). The two smallest juveniles were found on 1 and 4 July at SJ and have SVLs of 15.5 and 16.0 and masses of 0.3 each.

Vanzolinius discodactylus (Boulenger)

Three individuals are from TL and one from NTL; the latter and one of the former were on the forest floor by day. The others were at the edge of a temporary pond, a female by day and a calling male at night. The call is a series (usually 3) of whistlelike notes. An adult male has a SVL of 28.5 and a mass of 1.9, and an adult female has a SVL of 33.6 and a mass of 2.4; two juveniles have SVLs of 18.9 and 24.2 and masses of 0.7 and 1.3. In life, coloration of an adult male (KU 222100) was: Dorsum brown with dark brown markings; throat gray with black flecks; belly creamy white with gray flecks; tint of yellow in groin; iris bronze with black flecks.

MICROHYLIDAE

Chiasmocleis bassleri Dunn

Ten individuals fell into pitfall traps at night in the study zone at NTL. Four males have SVLs of 16.8–20.3 ($\bar{x}$ = 18.7) and masses of 0.5–1.0 ($\bar{x}$ = 0.75); six females with small ovarian eggs have SVLs of 19.5–21.6 ($\bar{x}$ = 20.3) and masses of 0.7–1.0 ($\bar{x}$ = 0.9). Coloration in life (KU 222103–05): Dorsum dull brown; canthal stripe prominent, cream; postorbital stripe creamy orange; forearm and stripe on anterior surface of hind limb pale orange; throat and chest gray with white flecks; belly and ventral surfaces of hind limbs white with pale bluish tint and large black spots; iris reddish bronze with minute black flecks. All individuals have a black inguinal spot, but they lack the indistinct pink spots on the flanks and anterior surfaces of the thighs in specimens from Santa Cecilia, Ecuador (Duellman, 1978).

Microhylidae *incerta sedis*

A single female (KU 222108) that was in a pitfall trap at 0950 on 20 July in the study zone at NTL does not fit into any of the genera of neotropical microhylids as characterized by Zweifel (1986) and modified by de Sá and Trueb (1991). A tympanum is present, and the occipital dermal fold is absent. There are three functional digits on the hand and four on the foot. In life, the dorsum was brown with minute cream flecks, the venter gray with white flecks, and the iris reddish bronze with black flecks (Pl. 1). Measurements: SVL 17.8, tibia length 7.5, foot length 7.1, head length 5.2, head width 5.5, diameter of eye 1.8, diameter of tympanum 0.8.

Radiographs revealed the existence of eight presacral vertebrae, coccygeal processes, small clavicles about one half length of coracoids, and quadratojugal separate from maxilla. The alary processes of the premaxillae seems to be inclined anteriorly, and there does not seem to be a notch in the shelf of the premaxillae. The skull appears to be completely roofed. The nature of the vomers and neopalatines could not be determined. The phalangeal formula for the hand is 1–2–3–2 and for the foot, ?–2–3–4–3 (first digit could not be determined); the terminal phalanges are pointed.

The only genera of New World microhylids having the occipital fold absent, clavicle reduced, and quadratojugal separate from maxilla (all derived character states according to Zweifel, 1986) are *Arcovomer, Chiasmocleis,* and *Syncope. Arcovomer* differs from the present specimen by lacking a tympanum and coccygeal processes and by having a normal phalangeal formula and T-shaped terminal phalanges. *Chiasmocleis* differs by lacking a tympanum and by having a normal phalangeal formula; however, some external digital reduction has been noted in occasional specimens of *Chiasmocleis* (Nelson, 1975).

Externally, the specimen resembles *Syncope,* but it is much larger than the two known species—SVL in *S. antenori* to 13.2 in females (Walker, 1973), to 11.7 in females of *S. carvalhoi* (Nelson, 1975). *Syncope antenori* has a tympanum, whereas *S. carvalhoi* does not. Externally, *S. antenori* has four fingers and four toes, and *S. carvalhoi* has three fingers and four toes. The phalangeal formula of *S. antenori* is 2–2–3–3 and 1–2–3–4–3; the phalangeal formula of *S. carvalhoi* is unknown. However, *Syncope* has only seven presacral vertebrae, as opposed to eight in the present specimen.

Thus, the present specimen exhibits characters of *Chiasmocleis* (eight presacral vertebrae) and *Syncope* (reduced phalangeal formula). Furthermore, it shares the presence of an external tympanum with *S. antenori;* the tympanum is absent in *Chiasmocleis* and *S. carvalhoi.* The specimen could be allocated to *Syncope* by amending the definition of that genus to include eight presacral vertebrae. The combination of states of *Chiasmocleis* and *Syncope* might justify the recognition of only one genus. However, no such taxonomic decisions should be forthcoming until more material is available on which to base a formal description of the species and to provide adequate osteological preparations so that some of the osteological characters can be verified.

RANIDAE

***Rana palmipes* Spix**

One adult was observed at the lagoon at SJ and two adult males having SVLs of 93.1 and 98.0, and masses of 79 each were on the shore of the oxbow lake at TL at night.

PLETHODONTIDAE

***Bolitoglossa peruviana* (Boulenger)**

Two females having SVLs of 31.2 and 36.4 were on leaves of bushes about 1.5 m above ground at the edge of the forest pond at NTL on the night of 20 July. At night the dorsum was pale tan; by day it was reddish brown with darker brown markings, and the venter was black. These specimens agree well with the definition of the species provided by Crump (1977), except that they have darker venters.

CAECILIAIDAE

***Caecilia tentaculata* Linnaeus**

One female having a total length of 615 and 124 primary annuli was moving on the forest floor during a heavy rain at 2215 hr on 23 July in the study zone at NTL. Two other individuals, an adult and a juvenile, were observed on the same night.

GEKKONIDAE

***Gonatodes concinnatus* (O'Shaughnessy)**

One adult female having a length of 44 + 34 (tail tip apparently regenerated) and a mass of 2.0 was active on a fallen log at night at SJ. Color notes on female (KU 222138): dorsum tan and brown; throat bluish white with chocolate brown streaks; belly dull yellow with brown streaks.

***Gonatodes humeralis* (Guichenot)**

One juvenile having a length of 32 + 22 and mass of 0.15 was found on a wall of a building in camp at TL by day.

***Hemidactylus mabouia* (Moreau de Jonnès)**

An adult male having a length of 62 + 71 and a mass of 3.7 was on a building in camp at SJ by night and a juvenile having a length of 25 + 27 was on a building there by day. One juvenile having a length of 23 + 26 and a mass of 0.1 was inside a building at TL by day.

***Lepidoblepharus hoogmoedi* Avila-Pires**

Two gravid females each having SVLs of 27 and one with a complete tail length of 25 were collected on, and under, palm litter near the temporary pond at TL; their masses were 0.45 and 0.40, respectively. An adult male having a SVL of 26, an incomplete tail, and a mass of 0.3 was in a pitfall trap by day in the study zone at NTL. These specimens match

closely the description and photograph provided by Avila-Pires (1995) in details of both scutellation and coloration, with the exception that the lower postnasal is about equal in size to the upper postnasal in the male (KU 222143).

Color notes on the male (KU 222143), in life: chin pinkish tan with dark brown stripes. Color notes on same specimen taken from color transparency: limbs dark brown; dorsum dark brown with two longitudinal rows of ill-defined pale brown blotches; top of head dark brown with diffuse blue-gray W-shaped mark between and covering eyelids; snout pale brown with dark brown spots, demarcated by thin cream transverse bar; cream horseshoe-shaped collar extending from posterior margin of orbits over occiput; dorsolateral pale brown stripes extending from occipital collar posteriorly onto anterior one fourth of tail; tail pale brown, distinctly paler than all other surfaces; all surfaces speckled with blue-gray scales, those on limbs forming discrete spots; those on tail forming diffuse stripe laterally on proximal part of tail; two cream postorbital bars extending from orbit onto throat; iris dull brown, unmarked.

In preservative, the throat of KU 222143 is cream with a complex series of bold transverse and longitudinal gray lines that extend laterally to become infralabial bars; the ventral scales are gray, becoming darker peripherally and the scales which comprise the escutcheon are white with dark edges. In preservative, the females (UPR-WED 60335, UPR-WED 60438) are uniform dark brown with cream throats that have bold, or indistinct, linear markings, respectively.

Dixon and Soini (1986) listed *Lepidoblepharus festae* as part of the herpetofauna of the Iquitos region. Their color notes for *L. festae* are similar to the pattern in the original description and that of specimens of *L. hoogmoedi* reported here, with the exception that their specimens from near Iquitos have additional dorsal and lateral lines. Inasmuch as Miyata (1985) questioned the applicability *L. festae* for populations in the Amazon basin and given that only five specimens have been reported (2 by Avila-Pires, 1995, plus the 3 reported herein), it is possible that when variation in *L. hoogmoedi* is more completely known, the population in the Iquitos region will be found to be referable to this species.

Pseudogonatodes guianensis Parker

One gravid female having a SVL of 26 was in a pitfall trap by day in the study zone at SJ. A gravid female having a SVL of 26 and a mass of 0.2 was in a pitfall trap in the study zone at NTL; each contained one egg.

Thecadactylus rapicauda (Houttuyn)

An adult female having a length of 111 + 65 was found on a palm trunk 1.5 m above the ground at night in the study zone at SJ. An adult male having a length of 103 + 66 and a mass of 26.0 was found on tree trunk at night in the study zone at NTL.

HOPLOCERCIDAE

Enyalioides cofanorum Duellman

One adult male having a length of 215 + 140 and a mass of 60 was sleeping (head up) on a small tree trunk at night in the study zone at SJ. Coloration in life of KU 222163 from color transparencies: Dorsum dull tan with irregular dark brown markings tending to form transverse bars; throat bluish gray; iris brown medially, orange-tan peripherally. This individual is somewhat duller in coloration than the type series from Santa Cecila, Ecuador (Duellman, 1973b).

Enyalioides laticeps (Guichenot)

One adult female having a length of 135 + 236 and a mass of 85.0 was on a tree trunk 2 m above the ground by day in the study zone at SJ. A juvenile having a length of 80 + 127 and a mass of 17.5 was sleeping on the ground under a small herb at night in the study zone at NTL. Color notes on the adult female (KU 222164): dorsum green; chin greenish yellow; throat rust; venter creamy tan; iris cream. Color notes on the juvenile (URP-WED 60106): dorsum bright green with dark rusty brown markings; throat buff with rusty red streaks; rest of venter cream with rusty red flecks; iris dull reddish copper with cream ring peripherally.

POLYCHROTIDAE

Anolis bombiceps Cope

Two adult females having lengths of 58 + 108 and 68 + 117 are from the study zone at NTL; the former female had a mass of 3.9 and was sleeping on a leaf 0.5 m above the ground, and the latter was killed by ants in a pitfall at night. Two adult males from the study zone NTL having lengths of 54 + 100 and 60 + 118 and masses of 2.8 and 3.3, respectively, were sleeping on leaves at night 0.3–0.5 m above the ground. Color notes on female (KU 222145): lining of buccal cavity and dewlap dark blue.

The distribution of *Anolis bombiceps* is encompassed completely within the western part of the range of *A. nitens*. These two species seem to be ecological equivalents; both are terrestrial and seem to favor logs and low buttresses. Both species have been reported from Río Itaya (Vanzolini and Williams, 1970) and Centro Unión (Dixon and Soini, 1986) in Departamento Loreto, Peru. Lescure and Gasc (1986) erroneously reported *A. bombiceps* from Santa Cecilia, Ecuador, where *A. nitens* is common (Duellman, 1978).

Anolis fuscoauratus D'Orbigny

This species was relatively common in the study zones at SJ, and NTL, along the stream at TL, and in the floodplain forest at TL. Individuals were inactive on saplings and leaves 0.5–2.0 m above the ground at night. One individual was asleep at night on emergent vegetation in the forest swamp at SJ. Ten females have lengths of 42–48 ($\bar{x}$ = 44.8) + 81–97 ($\bar{x}$ = 86.1) and masses of 0.8–1.5 ($\bar{x}$ = 1.2).

Six males have lengths of 38–48 ($\bar{x}$ = 43.5) + 74–87 ($\bar{x}$ = 82.5) and masses of 0.9–1.5 ($\bar{x}$ = 1.1). Two juveniles have lengths of 34 + 67 and 25 + inc. and masses of 0.5 and 0.2, respectively. Color notes on male (KU 222149): dewlap dull rose with pale cream scales. Color notes on male (KU 622152): dewlap pinkish rose with cream scales. In alcohol, two adult females (KU 222155, URP-WED 60416) are dark brown dorsally with a broad copper dorsal stripe, extending from the occiput well onto the tail and bordered laterally by thin black stripes.

Unlike as in most anoles, the dewlap color seems to be highly variable. In specimens from Santa Cecilia, Ecuador, the dewlap is rose-pink with white scales (Duellman, 1978), whereas in the Iquitos region of Peru, the dewlap is pale lemon yellow to pale green (Dixon and Soini, 1986). According to Avila-Pires (1995) the dewlap has been reported as red in specimens from Manaus, Brazil, and gray in specimens from Benjamin Constant, Amazonas, Brazil. However, in all specimens the scales in the dewlap are white or pale cream.

In her review of the habits of this species, Avila-Pires (1995:63) noted that "...*A. fuscoauratus* is mainly found on vegetation, up to 2 m, in forest, occasionally also on the ground or higher up (at least up to 5 m)." She mentioned that Beebe (1944) reported two specimens in the top of a 90-foot tree within 15 minutes after it had been cut down and suggested "...that the species also may be present in the canopy." Beebe's report and Avila-Pires's suggestion have been corroborated by observations of many individuals of *A. fuscoauratus* on branches and limbs at heights of 30 m above the ground along the canopy walkway at the Amazon Center of Environmental Education and Research near the junction of the Río Sucusari and Río Napo, Departamento Loreto, Peru (WED, pers. obs.).

Anolis nitens (Wagler)

An adult male having a length of 74 + 155 was at the edge of the forest at SJ by day and an adult female having a length of 83 + 171 and a mass of 16.0 was sleeping on a branch 0.5 m above the ground at night at SJ. The male (KU 222147) emitted an audible squeak while it was being restrained for a photograph. Vocalization has been reported in several species of *Anolis* (Greene, 1988), but never has it been reported in this species.

Previously, populations of this taxon in Amazonian Ecuador and Peru have been known as *Anolis chrysolepis* (subspecies *scypheus*) (Duellman, 1978; Dixon and Soini, 1986). Avila-Pires (1995) placed all subspecies of *A. chrysolepis* as subspecies of *A. nitens*. Geographically separate populations of *Anolis chrysolepis* (= *nitens*) were studied by Vanzolini and Williams (1970), together with *A. bombiceps*, which is sympatric with *A. nitens* in Vaupés, Colombia, and Loreto, Peru; they regarded the separate populations as subspecies, but, as pointed out by Avila-Pires (1995), areas of intergradation are not known between some of these populations. Thus, the "subspecies" of *A. nitens* may be distinct species, in which case the lizards in Amazonian Peru and Ecuador would be recognized as *Anolis scypheus* Cope.

Anolis trachyderma Cope

An adult male from the study zone at SJ having a length of 49 + 101 and a mass of 1.6 and an adult male from the study zone at NTL having a length of 54 + inc. and a mass of 2.3 were caught in a pitfall traps by day. A juvenile having a length of 31 + 55 and a mass of 0.2 was found on the forest floor by day in the study zone at NTL and a juvenile having a length of 34 + 60 and a mass of 0.9 was found climbing up the base of a stilt palm by day in the floodplain forest at TL. Color notes on a juvenile (URP-WED 60183): belly yellow; throat orange. All individuals have smooth ventral scales (*contra* Dixon and Soini, 1986).

Anolis transversalis Duméril

All individuals of this species were in the study zone or forest swamp at SJ. Two adult males having lengths of 77 + 150 and 76 + 142 and masses of 4.1 and 7.9, respectively were sleeping on horizontal vines 1.5–2.5 m above the ground at night. A juvenile having a length of 38 + 71 and a mass of 0.8 was in a pitfall trap by day and another juvenile having a length of 57 + 77 was sleeping on the tip of a vertical stem 2.5 m above the ground at night. Duellman (1978) and Dixon and Soini (1986) mentioned that this species typically seems to inhabit the high canopy level of large trees—perhaps only leaving these trees to lay eggs (Dixon and Soini, 1986). Our discovery of adult males and moderately -sized juveniles at heights of 1.5–2.5 m suggests that this species may be slightly more catholic in its choice of habitat. Color notes on a juvenile (KU 222161): iris blue; dewlap yellow-orange with dark brown markings; dorsum green with paler green and black diagonal markings. Color notes on an adult male (KU 222162): capable of changing from bright green with nearly black transverse markings to pale brown with less intense markings; iris blue.

TROPIDURIDAE

Tropidurus plica (Linnaeus)

An adult female having a length 122 + 146 (tail tip regenerated) and mass of 81.0 was on a tree trunk 5 m above the ground by day in the study zone at NTL.

Tropidurus umbra (Linnaeus)

All individuals were sleeping, head up or horizontally, on vegetation at night 0.5–5 m above the ground at night in the study zones at SJ and NTL, along the stream at TL, and in floodplain forest at TL, except one, which was in a pitfall by day in the study zone at SJ. Four adult males have lengths of 79–85 ($\bar{x}$ = 83.3) + 186–190 ($\bar{x}$ = 188.3) and masses of 15.1–18.5 ($\bar{x}$ = 16.7). A juvenile has a length of

69 + 155 and mass of 8.7. An adult female has a length of 84 + 187 and a mass of 15.5.

GYMNOPHTHALMIDAE

***Alopoglossus atriventris* Duellman**

Two females having lengths of 51 + 67 and 49 + 7 were in the study zone at SJ. The former was found in the leaf litter by day and had a mass of 4.5. The latter was killed by ants in a pitfall trap, and mass was not measured. One individual (URP-WED 60056) has black on the lateral surfaces, whereas the other (KU 222167) has the lateral surfaces only slightly darker brown than the dorsum; females of this species typically have lateral surfaces the same color as the dorsum (Duellman 1973b). Both specimens have cream venters, as is typical for females of this species.

***Alopoglossus buckleyi* (O'Shaughnessy)**

Two males having lengths of 47 + 79 and 43 + 69 and masses of 2.4 and 1.8, respectively, were on the forest floor by day in the study zone at NTL.

***Alopoglossus copii* Boulenger**

An adult male having a length of 58 + 103 and a mass of 6.0 was active at night in leaf litter immersed at the edge of the forest pond at NTL. It is possible that the lizard was sleeping and disturbed by footsteps. Color notes on adult male (KU 222169):top of head reddish brown; dorsum dull brownish black; venter creamy tan (Fig. 16). This species is known from only a few other specimens from the Amazonian slopes of the Andes in Ecuador (Ruibal, 1952; Peters and Orejas-Miranda, 1986) (but see below). The specimen reported here has the following scale counts (format following Ruibal, 1952): midbody 18; transverse dorsal rows 23; transverse ventral rows 19; gulars 8. There are 16/16 femoral pores, the two most median pores are preanal in position. The color pattern on this specimen matches closely that described by Ruibal (1952), except that a few ventral scales lack brown flecking on the anterior portion of the scale.

Fig. 16. *Alopoglossus copii,* KU 222169, adult male, 58 mm SVL.

Vanzolini (1986) listed *A. copii* as a synonym of *Leposoma southi* (fide Uzzell and Barry, 1971). In fact, Uzzell and Barry (1971) did not synonymize these two taxa; rather they referred two specimens reported as *A. copii* by Boulenger (1913) to *L. southi.* Lescure and Gasc (1986) reported *A. copii* from Colonia, Departamento Loreto, Peru. However, it is not clear that their specimens have been identified correctly, inasmuch as they also listed material reported as *A. copii* from Santa Cecilia, Ecuador, by Duellman (1978). All specimens of "*A. copii*" from Santa Cecilia subsequently have been identified as *A. angulatus* by T. C. S. Avila-Pires.

***Arthrosaura reticulata* (O'Shaughnessy)**

One adult male having a length of 47 + 60 and a mass of 2.3 was in a pitfall trap by day in the study zone at SJ. A juvenile having a length of 23 + inc. and mass of 0.1 was in leaf litter by day in the study zone at NTL and another juvenile having a length of 31 + inc. and a mass of 0.4 was in leaf litter at night near the temporary pond at TL. Color notes on adult male (KU 222170): venter orange-buff.

***Leposoma parietale* (Cope)**

This species was relatively common in the study zones at SJ and NTL; none was observed in the floodplain forest at TL. Most were in pitfall traps by day; a few were in leaf litter by day, and one was on floating leaves at night at the edge of the forest swamp at SJ . Three adult males had lengths of 32–37 ($\bar{x}$ = 34.6), all with incomplete tails, and masses of 0.6–0.8 ($\bar{x}$ = 0.7). Five adult females with complete tails had lengths of 34–38 ($\bar{x}$ = 36.2) + 41–54 ($\bar{x}$ = 49.8) and masses of 0.3–0.9 ($\bar{x}$ = 0.65); one female with an incomplete tail had a SVL of 44 and a mass of 1.5. Color notes on an adult female (KU 222174): venter dull cream.

***Neusticurus ecpleopus* Cope**

One adult male having a length of 50 + 80 drowned in a flooded pitfall trap at the edge of the lagoon at night in the study zone at SJ. An adult female having a length of 47 + 69 and a mass of 2.2 was active on floating leaves at the edge of a small *Heliconia* swamp at night in the study zone at NTL. Two juveniles having lengths of 27 + 20 (tail regenerating) and 24 + 32 and masses of 0.3 and 0.1, respectively, were in leaf litter and along a stream by day in the study zone at NTL. In alcohol, one juvenile (URP-WED 60101) has a white venter and the other juvenile (KU 222179) has a black venter. The dorsum of juveniles is pale tan; this color extends onto the tail. The dorsum of adults is uniform dark brown.

***Prionodactylus oshaugnessyi* Boulenger**

Two adult males having lengths of 39 + inc. and 40 + 93 are from the study zone at SJ; one was in leaf litter by day and the other on a log 0.2 m above the ground by day. A juvenile having a length of 21 + inc. and a mass of 0.3 was crawling up a sapling 1.5 m above the ground by day in the

study zone at SJ. A juvenile having a length of 24 + 46 was on the forest floor by day in the study zone at NTL. Color notes on a juvenile (URP-WED 59883): tail red. These specimens match closely the diagnosis for this species given by Avila-Pires (1995), but we concur with her comment that the status of this species with respect to *P. argulus* (Peters) needs further attention.

SCINCIDAE

***Mabuya nigropunctata* (Spix)**

Two juveniles having lengths of 132 + 39 and 50 + inc. and masses of 2.6 and 0.5 were on the ground in the camp at TL by day. These specimens match closely Avila-Pires's (1995) account for the species, which she recognized as separate from *M. bistriata* (Spix). However, the pale stripes bordering the dark lateral bands are more prominent than she presented as typical for the species. Also, these specimens lack keels on the scales, as seems to be characteristic of *M. nigropunctata* from western Amazonia, but these specimens are juveniles, and such ornamentation simply may not have developed. Color notes on juvenile (URP-WED 60102): head and dorsolateral stripes pale bronze-yellow; tail brown. According to Avila-Pires (1995), the tail is blue in this species.

TEIIDAE

***Kentropyx pelviceps* Cope**

This species was relatively common; individuals were observed at SJ, NTL, and all areas near TL. Most were on the forest floor by day, but one was sleeping on a leaf 0.5 m above the ground at night. Five adult females had lengths of 92–117 ($\bar{x}$ = 104.4) + 94–236 ($\bar{x}$ = 160.8) and masses of 22–37.6 ($\bar{x}$ = 28.7). Five adult males had lengths of 100–116 ($\bar{x}$ = 106.4) + 150–259 ($\bar{x}$ = 197.7) and masses of 27.5–46 ($\bar{x}$ = 32.9). Two juveniles had lengths of 60 + 137 and 75 + 155; the former had a mass of 8.0.

***Tupinambis teguixin* (Linnaeus)**

One male having a length of 202 + 395 and a mass of 250 was in a clearing created by a treefall at SJ. Another individual was observed in the forest at NTL.

AMPHISBAENIDAE

***Amphisbaena fuliginosa* Linnaeus**

Two females having lengths of 286 + 45 and 322 + 49 and masses of 17.1 and 21.5, respectively, were crawling across a road and through grass in camp by day at SJ.

BOIDAE

***Corallus enydris* (Linnaeus)**

This species was encountered only around the margin of the swamp at SJ. An adult female has a length of 1510 + 366, a mass of 650, 285 ventrals, and 122 subcaudals. An adult male has length of 1280 + 292, a mass of 375, 284 ventrals, and 112 subcaudals. Two juveniles have lengths of 591 + 142 and 509 + 120 and masses of 32.5 and 20.1, respectively; each has 284 ventrals, and they have 119 and 117 subcaudals, respectively. Both adults were in hunting postures on vines 0.4–0.5 m above the ground at night. One juvenile was crawling across a road at night. Color notes on juvenile (KU 222190): dorsum grayish-brown with faint blotches; venter salmon; iris cream.

COLUBRIDAE

***Chironius scurrulus* (Wagler)**

An adult female with a length of 1690 + 740, a mass of 1334, 157 ventrals, and 108 subcaudals was sleeping at night in small tree 1.5 m above the water at the edge of the swamp at SJ. Dissection revealed no food items or developing ova, but the body cavity contained many nematodes. Color notes (KU 222192): dorsum reddish brown; belly dull salmon with yellowish tint on chin; iris dark brown.

***Dipsas catesbyi* (Sentzen)**

An adult female containing four well-developed eggs and having a length of 550 + 203, a mass of 36.6, 186 ventrals, and 100 subcaudals was crawling on the ground at night in the study zone at SJ. An adult male having a length of 470 + 184, a mass of 15.5, 192 ventrals, and 104 subcaudals was crawling up a sapling 0.3 m above the ground at night in the study zone at NTL.

***Drymarchon corais* (Boie)**

A large adult (length ± 2.5 m) was observed moving rapidly across the forest floor by day in the study zone at SJ.

***Imantodes cenchoa* (Linnaeus)**

Eight individuals were collected in the study zones at SJ and NTL, the swamp at SJ, and the floodplain forest at TL. Four males have lengths of 744–798 ($\bar{x}$ = 779) + 322–365 ($\bar{x}$ = 339). Males have 263–285 ($\bar{x}$ = 273) ventrals and 162–180 ($\bar{x}$ = 169) subcaudals. Two adult females have lengths of 705 + 284 and 776 + 321, 259 and 267 ventrals, incomplete and 160 subcaudals, and masses of 21.5 and 24.0, respectively. One female contains two well-developed eggs. Of two juveniles, one was alive and the other smashed on a trail. With the exception of the latter, all were active on vegetation 0.3–3.0 m above the ground at night. Two adults each contained two *Anolis fuscoauratus* in their stomachs and one contained one *A. fuscoauratus*.

***Imantodes lentiferus* (Cope)**

One adult male having a length of 641 + 289, 235 ventrals, and 142 subcaudals was coiled in a tree by day at SJ.

A gravid female having a length of 645 + 285, a mass of 15.5, 231 ventrals, and 147 subcaudals was active on vegetation at night in the study zone at NTL; this snake contained two well-developed eggs.

Leptodeira annulata (Linnaeus)

Two adult males having lengths of 404 + 149 and 514 + 187 (mass of latter male: 29.5) were active at night on vegetation along the edge of lagoon at SJ while frogs were chorusing. These individuals have 189 ventrals and 93–94 subcaudals. One individual contained two nearly digested, unidentified frogs in the digestive tract.

Oxyrhopus petola (Reuss)

One adult male having a length of 674 + 178, a mass of 22.0, 217 ventrals, and 123 subcaudals was found in the study zone at NTL. Another adult male having a length of 649 + 246, a mass of 64.0, 215 ventrals, and 123 subcaudals was at the forest pond at NTL. An adult female having a length of 835 + 253, a mass of 122.0, 213 ventrals, and 100 subcaudals was in the floodplain forest at TL. The dorsum of the former male is black with bands; all bands are immaculate red except the three anteriormost bands, which are white. In the latter male all pale bands are immaculate red (Fig. 17). The female has a black dorsum with red bands that are heavily flecked with black. All specimens have 14 bands on the body that are narrower than the black interspaces. The venters of all three specimens are cream. All individuals were active on vegetation 0.5–3.5 m above the ground at night.

Fig. 17. *Oxyrhopus petola,* KU 222200, adult male, 649 mm SVL. Note that the nape band is the same color as the pale bands on the body.

Taeniophallus brevirostris (Peters)

We follow Myers and Cadle's (1994) assignment of *Echinanthera* (= *Rhadinaea*) *brevirostris* to the genus *Taeniophallus* Cope. One adult male having a length of 282 + 83, a mass of 12.6, 162 ventrals, and 64 subcaudals was active on the forest floor by day in the study zone at NTL. Color notes (KU 222203): throat, anterior part of venter lemon-yellow, rest of venter white.

Umbrivaga pygmaea (Cope)

One female having a length of 192 + 42 was dead on a dirt road in the morning at SJ. This specimen has 126 ventrals and 32 subcaudals.

Xenopholis scalaris (Wucherer)

Two adult females having lengths of 295 + 47 and 278 + 55, masses of 11.5 and 11.0, 144 and 143 ventrals, and 31 and 37 subcaudals, respectively, are from the study zone at NTL; the latter contains two well-developed eggs. Both individuals were active on the forest floor at night, and each displayed conspicuous body-flattening behavior when handled (Fig. 18).

ELAPIDAE

Micrurus spixii (Jan)

One adult male having a length of 1210 + 58, a mass of 530.0, 109 ventrals, and 17 subcaudals was active on the forest floor by day in the study zone at NTL.

VIPERIDAE

Bothrops atrox (Linnaeus)

A juvenile having a length of 392 + 69, a mass of 25.4, 196 ventrals, and 70 subcaudals, and an adult male having a length of 1060 + 182, a mass of 360.0, 202 ventrals, and 71 subcaudals are from the study zone at SJ. The juvenile was active on the forest floor at the edge of the lagoon at night and contained the remains of an unidentifable frog in the digestive tract. The adult was on the forest floor by day; it contained the remains of a small, unidentifable rodent in the digestive tract. A juvenile having a length of 400 + 58, a mass of 28.0, 206 ventrals, and 64 subcaudals was coiled on a fallen palm frond at the edge of the forest pond at NTL at night.

Bothrops brazili Hoge

A juvenile having a length of 394 + 62, a mass of 34.0, 177 ventrals, and 59 subcaudals was crawling on the forest floor by day in the study zone at NTL. This individual has 19 dark gray C-shaped marks on either side of the dorsum of the body; many are staggered on either side and do not meet at the midline. Distinct pale brown postocular stripes are

Fig. 18. *Xenopholis scalaris,* KU 222204, adult female, 295 mm SVL. Note that the posterior two thirds of the body is flattened.

present, and they are not bordered below by a dark stripe. In alcohol, the tip of the tail is pale; color in life was not recorded.

Porthidium hyoprora (Amaral)

An adult female having a length of 710 + 120, a mass of 500.0, 130 ventrals, and 48 subcaudals was coiled between the buttresses of a large tree at night in the study zone at SJ; it contained rodent hairs in the lower intestine. The subcaudal scales on this individual are single, except the distal three, which are paired. Color notes (KU 222208): dorsum grayish brown with reddish brown blotches dorsally and chocolate brown spots laterally; canthal stripe reddish brown; postorbital stripe dark brown; venter grayish tan with cream spots. During capture and subsequent handling this individual remained calm and sluggish; neither gaping nor tail vibrating behaviors were observed. A male having a length of 285 + 62, a mass of 26.0, 125 ventrals, and 49 subcaudals was crawling on the forest floor at night during a moderate rain in the study zone at NTL. The male has much greater contrast between the pale and dark areas on the dorsum than does the female (Fig. 19). Color notes on the male (KU 222209): dorsum tan with chocolate brown blotches becoming black on tail; venter predominately black with cream and rusty red spots; throat reddish brown with yellow spots. The male was much more aggressive during handling than the female; it struck repeatedly and vibrated the tail rapidly; gaping behavior was not observed. The size difference between these two adults is striking; the smaller male apparently is an adult (based on the large everted hemipenes). Campbell and Lamar (1989) noted that this species typically is found near water; however, both

Fig. 19. *Porthidium hyoprora:* Top—KU 222209, adult male, 285 mm SVL. Bottom—KU 222208, adult female, 710 mm SVL. Note near absence of pattern on anterior part of body of female.

of these specimens were in elevated, well-drained areas some distance (> 100 m) from flowing or standing water.

CHELIDAE

Phrynops gibbus (Schweigger)

One adult female was observed on the road near SJ. This individual had a small hole drilled near the edge of its carapace and may have originated from another area, having been brought in as a pet.

Platemys platycephala (Schneider)

One adult male was observed near the edge of the SJ lagoon.

PELOMEDUSIDAE

***Podocnemis unifilis* Troschel**

Three juveniles were brought into camp at SJ by a local inhabitant who had caught them about 3 km to the south, in the Río Tigre. This species was abundant in the oxbow lake at TL, where many large adults were observed.

ALLIGATORIDAE

***Caiman crocodilus* (Linnaeus)**

This species apparently was common—several individuals seen nightly—in the SJ lagoon and the SJ swamp. The largest individual observed had a total length of about 2.5 m. This species was not observed in any of the bodies of water around TL.

CROCODYLIDAE

***Paleosuchus palpebrosus* (Cuvier)**

One juvenile having a length of 257 + 203 and a mass of 300 was sitting on the muddy bottom of a clear pool in a small forest stream at NTL at night. Color notes based on color transparencies: Dorsum of body and tail orange-tan with dark brown transverse bars (ill-defined on body); limbs and flanks dull brown with individual cream scales on flanks, especially noticeable at insertion of forelimbs; top of snout between nostrils and eyes, occiput, and temporal region brownish black; venter cream with small brown spots laterally on posterior part of belly and rust edges to scales on throat; iris dull bronze-brown with minute brown flecks; sclera of eye pale blue.

BIOGEOGRAPHY

Despite the incomplete nature of the collections from San Jacinto and Teniente López, they reveal some interesting aspects about the herpetofauna in the upper Amazon Basin. Herein we provide general comments on the herpetofauna, comparisons of the three localities (grouped sites at SJ, TL, and NTL), comparisons of the study zones at SJ and NTL), and comparisons with other regions in the upper and central Amazon Basin. Most of the emphasis is placed on data on anurans and lizards, collections of which are far more extensive than of other groups. Snakes are notoriously difficult to sample in lowland tropical rainforest; we obtained only 15 species, but at least 50 species are to be expected in the region. No effort was made to sample aquatic habitats; thus, our data on turtles, aquatic snakes, and crocodilians are sparse. The diel activity, microhabitats, and sites of occurrence of 113 species are given in Table 1.

COMPARISONS AMONG SITES

Curves of species-discovery rates indicate that the faunas at SJ and NTL were sampled evenly. Seventy-five species were obtained in 36 person-days at the former and 75 species in 30 person-days at the latter (Fig. 20). Only 43 species were obtained at TL, where collecting effort was less (24 person days) and no drift fences and pitfall traps were used. Comparisons of the species-discovery rates at SJ and NTL with those at Santa Cecilia, Ecuador, where 173 (updated to 177) species were reported by Duellman (1978), and Cuzco Amazónico, Peru, where 145 species are known (Duellman and Koechlin, 1991), suggest that we obtained about 50% of the herpetofauna at SJ and TL. Our discovery of only 15 species of snakes, in contrast to 51 and 47 species at Santa Cecilia and Cuzco Amazónico, respectively, indicates that the principal group that is under-represented in collections from northern Loreto is snakes.

Comparisons of the herpetofaunas at the three sites were made using the coefficient of biogeographic resemblance of $2C/ N_1 + N_2$, where C = the number of species in common and N_1 and N_2 = the number of species at sites one and two, respectively (Duellman, 1990). This analysis reveals that there is greater similarity in the entire herpetofaunas, anurans only, and lizards only between SJ and NTL (40 km apart) than between TL and NTL (1.5 km apart) (Table 2). The similarities between SJ and NTL are highest among lizards (CBR = 0.67). Among anurans, TL shows a closer resemblance to SJ (CBR = 0.52) than NTL (CBR = 0.44), whereas, SJ and NTL are more nearly alike (CBR = 0.58). The discrepancies in anurans among sites most likely reflect differences in available breeding sites. The presence of the black-water lagoon at SJ and the oxbow lake at TL provided breeding sites for species such as *Hyla calcarata* and *Rana palmipes,* whereas suitable breeding sites for these species were absent at NTL. The floodplain at TL was the only place where *Colostethus trilineatus* and *Dendrophryniscus minutus* were found; these species seemed to shun the hilly regions at SJ and NTL.

Inexplicably, some species not dependent on specific breeding sites were abundant at one site and absent at others. For example, among the species in the *Eleutherodactylus conspicillatus* group, *E. lanthanites* was present only at SJ, whereas *E. peruvianus* and *E. malkini* were present at TL and NTL. Among lizards of the *Anolis nitens* group, *A. nitens* was present only at SJ and *A. bombiceps* only at NTL.

Nineteen species (12 anurans, 6 lizards, and 1 snake) are common to all three sites. Thus, of 114 species, only 16.7% were found at all three sites; these include 18.2% of the anurans, 25.0% of the lizards, and 6.7% of the snakes. Again, the data on snakes are insufficient to be meaningful.

The patchiness of habitats in the lowland tropical rainforest is exemplified by data from SJ and NTL. At the latter site, the forest pond is only about 150 m west of the study zone, in which no pond existed; 16 species, 13 of which are anurans, were found at the forest pond but not in the study zone. Likewise, at the swamp about 1.5 km SSW of the study zone at SJ, five species were found that were not collected or observed in the study zone. It is evident that small patches of appropriate habitat, especially breeding sites for anurans, are widely scattered in the forest; such small patches

Table 1. Occurrence of species of amphibians and reptiles at various sites at San Jacinto and Teniente López, Peru.—Diel Activity: DH = Diurnal and heliophylic; DS = Diurnal shade; N = Nocturnal. Microhabitat: A = Aquatic; AM = Aquatic margin; B = Bushes (< 1.5 m); E = Edificarian; F = Fossorial; G = Ground; LL = Leaf litter; TL = Tree limbs; TT = Tree trunks. Sites: CA = Camp (including forest clearing at San Jacinto), FL = Floodplain (including temporary pond), FP = Forest pond, LA = Lagoon, ST = Stream, SW = Swamp, SZ = Study zone. Occurrence: + = Present, – = Not recorded.

	Diel	Micro-	San Jacinto				Teniente Lopez				
Species	activity	habitat	Sz	La	Sw	Ca	Sz	Fp	Fl	St	CA
Anura: Bufonidae:											
Bufo marinus	N	G	+	–	–	+	–	–	–		+
Bufo typhonius "A"	DS	G	+	–	–	–	+	+	+	+	–
Bufo typhonius "B"	DS	G	+	–	–	–	–	–	–	+	–
Bufo typhonius "C"	DS	G	+	–	–	–	+	+	–	–	–
Dendrophryniscus minutus	DS	LL	–	–	–	–	–	–	+	–	–
Anura: Dendrobatidae:											
Colostethus trilineatus	DS	LL	–	–	–	–	–	–	+	–	–
Dendrobates ventrimaculatus	DS	LL	+	–	–	–	+	–	+	–	–
Epipedobates femoralis	DS	LL	+	–	–	–	+	–	–	–	–
Epipedobates hahneli	DS	LL	+	–	–	–	–	–	–	–	–
Epipedobates zaparo	DS	LL	+	–	–	–	+	–	–	–	–
Anura: Hylidae:											
Hyla albopunctulata	N	TL	+	–	–	–	–	–	–	–	–
Hyla boans	N	TL	–	–	–	+	–	–	–	+	–
Hyla brevifrons	N	B	–	–	–	–	–	–	+	–	–
Hyla calcarata	N	B	–	+	–	–	–	–	+	–	–
Hyla fasciata	N	B	–	–	+	–	+	–	–	–	–
Hyla geographica	N	TL	–	–	–	–	+	–	+	–	–
Hyla granosa	N	B	–	+	+	–	–	–	–	–	–
Hyla koechlini	N	B	–	–	–	–	–	+	–	–	–
Hyla lanciformis	N	B, TL	+	+	+	–	+	+	–	–	–
Hyla leucophyllata	N	B,TL	+	+	–	–	–	+	–	–	–
Hyla marmorata	N	TL	–	–	–	–	+	–	–	–	–
Hyla parviceps	N	B, TL	–	–	–	–	–	+	+	–	–
Hyla rhodopepla	N	B	–	–	–	–	–	+	–	–	–
Hyla riveroi	N	B	–	–	+	–	–	–	+	–	–
Hyla sarayacuensis	N	B	–	–	–	–	+	+	–	–	–
Osteocephalus buckleyi	N	TL		–	–	–	+	–	–	–	–
Osteocephalus cabrerai	N	TL	–	–	+	–	–	–	–	–	–
Osteocephalus leprieurii	N	B, TL	+	–	–	–	+	–	–	–	–
Osteocephalus planiceps	N	B, TL	+	+	+	+	+	–	+	–	–
Osteocephalus taurinus	N	TL	+	–	–	–	–	–	+	–	–
Osteocephalus sp.	N	TL	+	–	–	–	+	–	–	+	–
Phyllomedusa coelestis	N	TL	–	–	–	–	+	–	–	–	–
Phyllomedusa hulli	N	TL	–	–		–	–	+	–	–	–
Phyllomedusa tarsius	N	TL	+	–	–	–	–	+	–		–
Phyllomedusa tomopterna	N	TL	–	–	–	+	+	–	–	–	–
Phyllomedusa vaillanti	N	TL	+	+	–	–	+	–	+	–	–
Scinax cruentomma	N	B	–	–	–	–	–	–	+	–	+
Scinax funerea	N	B, TL	+	–	–	–	–	+	+	–	–
Scinax garbei	N	B	–	+	–	–	–	–	–	–	–
Scinax rubra	N	B, G	–	–	–	+	–	–	+	–	+
Anura: Leptodactylidae:											
Adelophryne tridactyla	N	G	+	–	–	–	+	–	–	–	–
Adenomera hylaedactyla	N	LL	+	–	–	–	+	–	+	–	–
Ceratophrys cornuta	N	G	–	–	–	–	–	–	+	–	–
Edalorhina perezi	DS	LL	+	–	–	–	+	–	–	–	–
Eleutherodactylus acuminatus	N	TL	–	–	–	+	–	–	–	–	–
Eleutherodactylus altamazonicus	N	B	–	–	–	–	–	–	+	–	–
Eleutherodactylus delius	N	B	+	–	–	–	–	–	–	–	–

Table 1. (cont.)

SPECIES	DIEL ACTIVITY	MICRO-HABITAT	SAN JACINTO				TENIENTE LOPEZ				
			SZ	LA	SW	CA	SZ	FP	FL	ST	CA
Eleutherodactylus diadematus	N	B	+	–	–	–	+	–	+	–	
Eleutherodactylus lanthanites	N	B	+	–	–			–	–	–	–
Eleutherodactylus luscombei	N	B	+	–	–	–	+	–	+	–	
Eleutherodactylus malkini	N	B	–	–	–		+	–	+	+	–
Eleutherodactylus martiae	N	B	+	–	–	–	+	–	–	–	–
Eleutherodactylus nigrovittatus	DS	LL	+	–	–	–	+	–	–	–	–
Eleutherodactylus ockendeni	N	B	+	–	–	–	+	–	+	–	–
Eleutherodactylus peruvianus	DS, N	B, G	–	–	–	–	+	–	+	–	–
Eleutherodactylus quaquaversus	N	B	–	–	–	–	+	–	+	–	–
Eleutherodactylus sulcatus	N	G	–	–	–	–	+	–	–	–	–
Ischnocnema quixensis	N	G	+		–		+		+	–	
Leptodactylus pentadactylus	N	G	+	+	–	+	–	+	+	–	–
Leptodactylus rhodomystax	N	G	–	–			+			–	–
Leptodactylus wagneri	N	G	–	–	–	+	+	+	–	–	–
Lithodytes lineatus	N	G	+			–	+	–		–	–
Physalaemus petersi	N	G	+	+	–	–	+	–	+	–	–
Vanzolinius discodactylus	N	G	–	–	–	–	+	–	+	–	–
Anura: Microhylidae:											
Chiasmocleis bassleri	N	G	–	–	–	–	+	–	–	–	–
Microhylidae sp.	N	G					+				–
Anura: Ranidae:											
Rana palmipes	N	AM	–	+	–	–	–	–	+	–	–
Caudata: Plethodontidae:											
Bolitoglossa peruviana	N	B	–	–	–	–	–	+	–	–	–
Gymnophiona: Caeciliaidae:											
Caecilia tentaculata	N	F	–	–	–	–	+	–	–	–	–
Sauria: Gekkonidae:											
Gonatodes concinnatus	DS	TT	+	–	–	–	–	–	–	–	–
Gonatodes humeralis	DS	E	–	–	–	–	–	–	–	–	+
Lepidoblepharus hoogmoedi	DS	LL	–	–	–	–	+	–	+	–	–
Pseudogonatodes guinanesis	DS	LL	+	–	–	–	+	–	–		–
Thecadactylus rapicauda	N	TT	+	–	–	–	+	–	–	–	–
Sauria: Hoplocercidae:											
Enyalioides cofanorum	DH	TT	+	–	–	–	–	–	–	–	–
Enyalioides laticeps	DH	TT	+	–	–	–	+	–	–	–	–
Sauria: Polychrotidae:											
Anolis bombiceps	DH	G	–	–	–	–	+	–	–	–	–
Anolis fuscoauratus	DS	B, TL	+	–	–	–	+	–	+	+	–
Anolis nitens	DH	G	+	–	–	+	–	–	–	–	
Anolis trachyderma	DS	B	+	–	–	–	+	–	+	–	–
Anolis transversalis	DH	TL	+	–	+	–	–	–	–	–	–
Sauria: Tropiduridae:											
Tropidurus plica	DH	TT	–	–	–	–	+	–	–	–	–
Tropidurus umbra	DH	TT	+		–	–	+	–	+	+	–
Sauria: Gymnophthalmidae:											
Alopoglossus atriventris	DS	LL	+	–	–	–	–	–	–		–
Alopoglossus buckleyi	DS	LL	–	–	–	–	+	–	–	–	–
Alopoglossus copii	DS	LL	–	–	–	–	–	+			–
Arthrosaura reticulata	DS	LL	+	–	–	–	+	–	+	–	–
Leposoma parietale	DS	LL	+	–	–	–	+	–	–	–	–
Neusticurus ecpleopus	DS	AM	+	–	–	–	+	–	–	–	–
Prionodactylus oshaugnessyi	DH	G	+	–	–	–	+		–	–	–
Sauria: Scincidae:											
Mabuya nigropunctata	DH	G	–	–	–	–	–	–	–	–	+
Sauria: Teiidae:											
Kentropyx pelviceps	DH	G	+	–	–	+	+	+	+	+	+

Table 1. (cont.)

SPECIES	DIEL ACTIVITY	MICRO-HABITAT	SAN JACINTO				TENIENTE LOPEZ				
			SZ	LA	SW	CA	SZ	FP	FL	ST	CA
Tupinambis teguixin	DH	G	–	–	–	+	+	–	–	–	–
Amphisbaenia: Amphisbaenidae:											
Amphisbaena fuliginosa	DS	F	–	–	–	+	–	–	–	–	–
Serpentes: Boidae:											
Corallus enydris	N	TL	–	–	+	–	–	–	–	–	–
Serpentes: Colubridae:											
Chironius scurrulus	DH	B, G	–	–	+	–	–	–	–	–	–
Dipsas catesbyi	N	B, TL	+	–	–	–	+	–	–	–	–
Drymarchon corais	DH	G	+	–	–	–	–	–	–	–	–
Imantodes cenchoa	N	B, TL	+	–	+	–	+	–	+	–	–
Imantodes lentiferus	N	B, TL	+	–	–	–	+	–	–	–	–
Leptodeira annulata	N	B, TL	+	+	–	–	–	–	–	–	–
Oxyrhopus petola	N	G, B	–	–	–	–	+	+	+	–	–
Taeniophallus brevirostris	DH	G	–	–	–	–	+	–	–	–	–
Umbrivaga pygmaea	?	G	–	–	–	+	–	–	–	–	–
Xenopholis scalaris	N	G	–	–	–	–	+	–	–	–	–
Serpentes: Elapidae:											
Micrurus spixii	DS	G	–	–	–	–	+	–	–	–	–
Serpentes: Viperidae:											
Bothrops atrox	DH, N	G, B	+	–	–	–	–	+	–	–	–
Bothrops brazili	DS	G	–	–	–	–	+	–	–	–	–
Porthidium hyoprora	N	G	+	–	–	–	+	–	–	–	–
Testudines: Chelidae:											
Phrynops gibbus	D	A	–	–	–	+	–	–	–	–	–
Platemys platycephala	D	A	–	–	–	+	–	–	–	–	–
Testudines: Pelomedusidae:											
Podocnemis unifilis	D	A	–	–	–	+[1]	–	–	–	–	–
Crocodylia: Alligatoridae:											
Caiman crocodilus	N	A	–	+	–	–	–	–	–	–	–
Crocodylia: Crocodylidae:											
Paleosuchus palpebrosus	N	A	–	–	–	–	+	–	–	–	–
Total Species:			55	12	10	16	63	22	33	8	6

[1] Río Tigre.

are easily overlooked in quick surveys of the herpetofauna. Thus, many species can be missed easily. Were it not for the discovery of the small forest pond at NTL, our tally for species at that locality would have been 63 instead of 79, and five species, including a new species of *Phyllomedusa,* would not have been recorded from northern Loreto.

COMPARISON OF STUDY ZONES

Sampling effort and protocol in the study zones at SJ and NTL were essentially equal, and most of the specimens were collected or observed in the study zones. Thus, more detailed analyses of the anurans and lizards in these zones are possible. A total of 48 species of anurans was found in the two study zones. Of these, 20 (42%) were found at both sites; 13 species (27%) were found only at SJ, and 15 species (31%) only at NTL. Among the 20 species common to both sites, there is a striking difference in the relative abundance (= frequency of capture and/or observation) of species (Fig. 21). An R X C test of independence (Sokol and Rohlf, 1981) shows a significant difference in relative frequencies between sites ($G = 149.47$, $df = 19$, $P < 0.001$).

A total of 21 species of lizards was found in the two study zones. Of these, 11 (52.3%) were found at both sites; six species (28.6%) were found only at SJ, and five (23.8%) only at NTL. Slight differences are evident in the relative abundances of the 11 species common to both sites (Fig. 22). An R X C test of independence (Sokol and Rohlf, 1981) reveals no significant difference between the sites ($G = 6.15$, $df = 10$, $P > 0.05$).

Based on the taxonomic composition and relative abundance of species, repeated sampling success can be predicted

Table 2. Species of amphibians and reptiles at three sites. Abbreviations in headings to columns correspond to sites in first column. The uppermost of the three numbers in each cell is the total herpetofauna, the middle number in each cell is that of anurans, and the lowermost number is that of lizards. The number of species at each site is shown in boldface in the common cell; the numbers of species that are in common to two sites are in the upper right, and the coefficient of biogeographic resemblance is in italics in the lower left.

SITE	SJ	TL	NTL
San Jacinto (SJ)	**75**	25	44
	44	20	27
	17	6	11
Teniente López (TL)	*0.42*	**43**	27
	0.52	**33**	18
	0.48	**8**	7
1.5 km N Teniente López (NTL)	*0.56*	*0.46*	**75**
	0.58	*0.44*	**45**
	0.67	*0.56*	**17**

by application of the rarefaction algorithm (Krebs, 1989), which extrapolates the number of species expected in a given sample size. For anurans, the curve is higher for TL than SJ (Fig. 23). Thus in a sample size of 50 specimens, 17 species would be expected at SJ and 21 species at NTL, whereas in a sample size of 100, 24 species would be expected at SJ and 30 at NTL. A sample size of 25 individuals of lizards from either site would be expected to contain 12 species.

Differences in species composition and relative abundances among anurans between the study zones seems to be attributable mostly to the presence of the lagoon at SJ. Several species of anurans (*Bufo marinus, Hyla albopunctulata, H. calcarata, H. granosa, Scinax garbei,* and *Rana palmipes*) not present at NTL were found only in that part of the study zone bordering the lagoon. The abundance of other species (*Hyla lanciformis, H. leucophyllata, Phyllomedusa vaillanti, Leptodactylus pentadactylus,* and *Physalaemus petersi*) at SJ was increased by their presence mainly near the lagoon. Thus, the presence of a breeding site utilized by many species of frogs skewed not only the presence, but also the abundance, of species at SJ. On the other hand, throughout the hilly region in the study zone at SJ fewer species of anurans (27) were found than in the equally hilly study zone at NTL (35).

The relative abundance of anurans with respect to diel activity and microhabitat differs between the study zones (Fig. 24). At both sites, the percentages of individuals that are nocturnal/arboreal and nocturnal/terrestrial are about equal, but these values are 44.6% and 41.2% respectively at SJ and 26.8% and 27.5% respectively at NTL. On the other hand, at SJ only 14.2% of the individuals are diurnal/terrestrial, as contrasted to 45.8% at NTL. This discrepancy, which also is reflected in the different percentages of nocturnal individuals at the two sites, is owing to the fact that at NTL the three most abundant species (*Bufo typhonius* "A", *B. typhonius* "C", and *Epipedobates zaparo*), which make up 33.6% of the total, are diurnal/terrestrial, whereas at SJ the most abundant species (*Physalaemus petersi,* 28.8%) is nocturnal/terrestrial, and the next two most abundant species (*Phyllomedusa vaillanti,* 13.3%, and *Hyla calcarata,* 10.2%) are nocturnal/arboreal.

Discrepancies exist between the two study zones with respect to diel activity and microhabitat among lizards

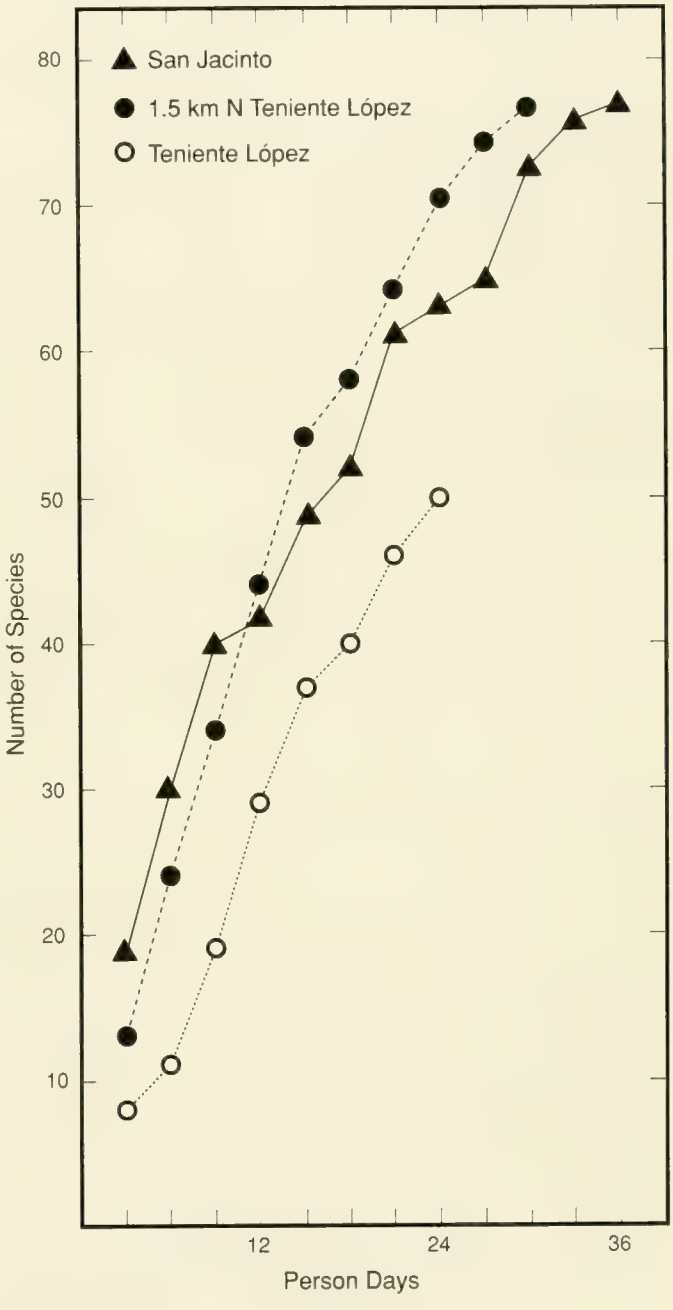


Fig. 20. Species discovery rates at three sites.

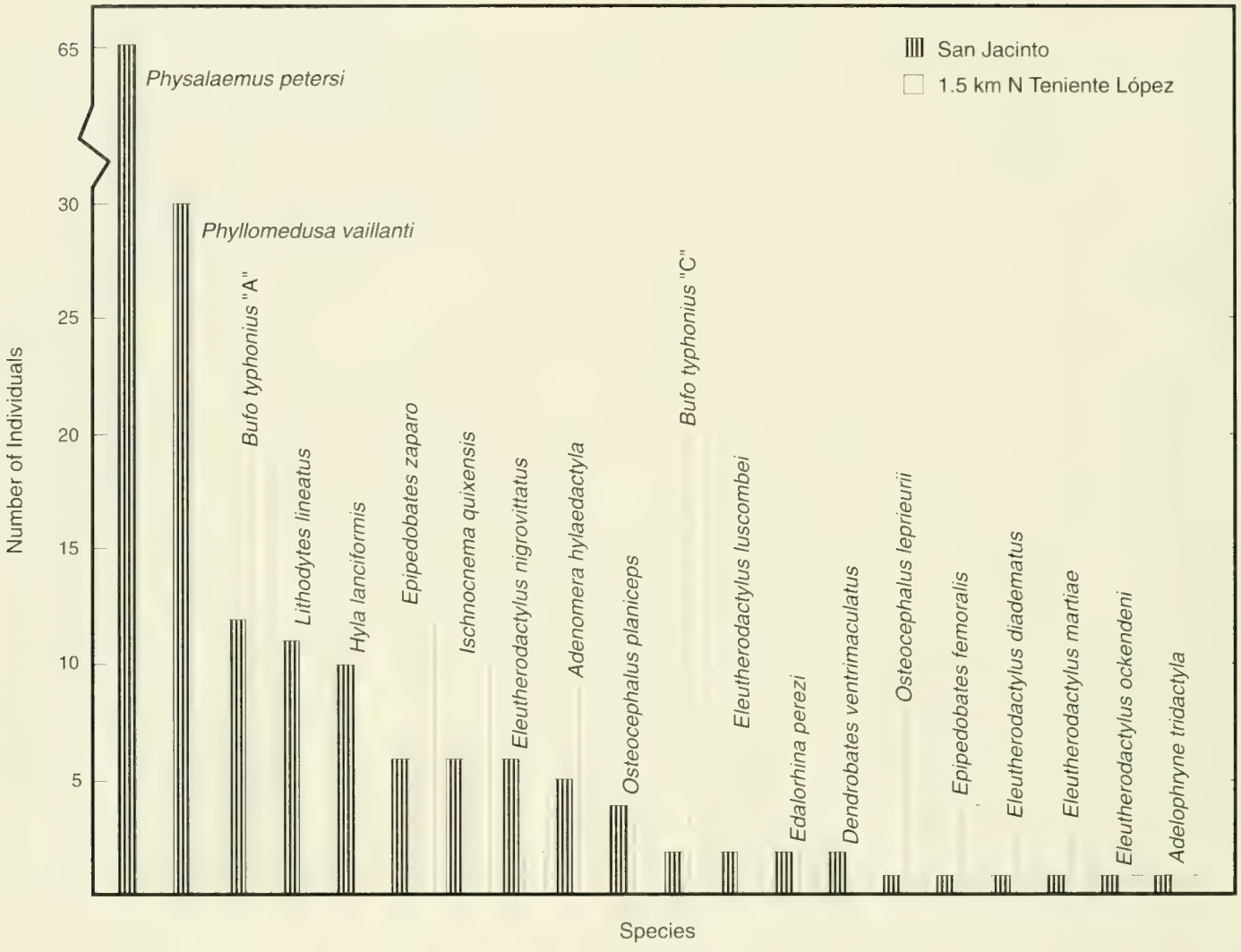


Fig. 21. Relative abundance of species of anurans in common to study zones at San Jacinto and at 1.5 km N of Teniente López.

(Fig. 25). Twice the percentage of diurnal/arboreal lizards (50% vs 25%) exists at SJ than as compared with NTL, and the percentage of diurnal/terrestrial lizards is greater at NTL (72.2%) than at SJ (47.4%). These differences are because of relative abundances of the most common species at the two sites—the diurnal/arboreal *Anolis fuscoauratus* (28.9% of total) at San Jacinto and the diurnal/terrestrial *Kentropyx pelviceps* (19.4%) at NTL. Only one lizard, *Thecadactylus rapicauda,* is nocturnal/arboreal; it is represented by one individual from each study zone.

The total mass of anurans is much higher at SJ (1307.5 g) than at NTL (658.7 g), but 240 g of this mass at SJ is one *Bufo marinus.* This species usually inhabits open, disturbed areas, such as the camp clearing; one large adult was in a pitfall trap in the quadrat closest to the clearing (and lagoon) and presumably wandered into the forest or swam across the lagoon. If that individual is removed, the total mass for SJ is 1067.5 g, and the mean mass per individual is 4.74 g, only slightly higher than the mean mass (4.33 g) for anurans at NTL. The total mass of lizards is 455.2 g at SJ and 342.9 g at NTL, and the mean mass is 11.98 g and 9.80 g, respectively.

When the single *Bufo marinus* is excluded, the distribution of mass among different diel activities and microhabitats roughly approximates the abundance of individuals (Table 3). For example, the two most common anurans (*Bufo typhonius* "A" and *B. typhonius* "C") at NTL have a combined mass of 257.9 g and make up 39.2% of the total mass of anurans and 97.9% of the mass of diurnal/terrestrial anurans there; the other six diurnal/terrestrial species represented by 31 specimens have a combined mass of only 5.6 g. At SJ, where the greatest amount of mass is of nocturnal/arboreal

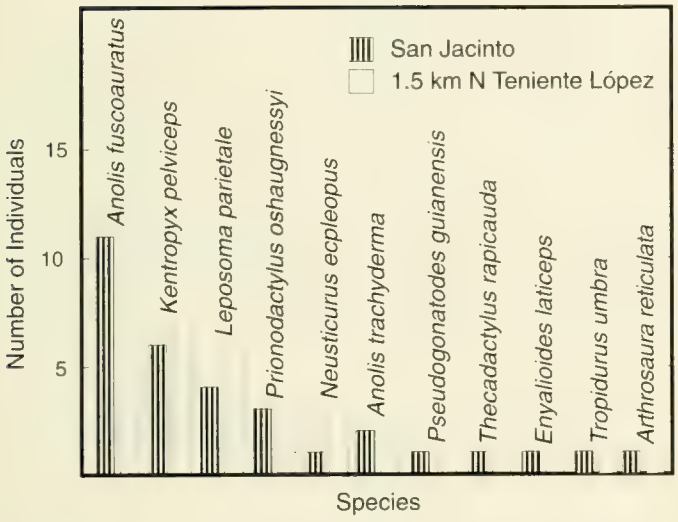


Fig. 22. Relative abundance of species of lizards in common to study zones at San Jacinto and at 1.5 km N of Teniente López.

anurans, the two species in this category (*Hyla lanciformis* and *Phyllomedusa vaillanti*) have a combined mass of 446.3 g and make up 41.8% of the total mass of anurans and 85.2% of the mass of nocturnal/arboreal anurans there; the other 15 nocturnal/arboreal species represented by 71 specimens have a combined mass of only 77.8 g. The most common species of anuran at SJ, *Physalaemus petersi*, is nocturnal/terrestrial; its mass of 87.0 g accounts for only 8.1% of the total mass of anurans at SJ.

Mass of lizards with respect to diel activity and microhabitat is proportionately the same at SJ and NTL. At both sites, *Kentropyx pelviceps* accounts for greatest amount of mass of lizards. At SJ and NTL, it accounts for 46.4% and 49.3% of the total mass of lizards, respectively, and 86.6% and 87.0% of the mass of diurnal, terrestrial lizards, respectively. The most abundant species at SJ is the small, diurnal/arboreal *Anolis fuscoauratus*, which accounts for only 2.4% of the total mass of lizards and 6.0% of the mass of diurnal/arboreal lizards there. Certainly, here is a case of abundance not correlating with mass; mean mass of other diurnal/arboreal lizards at SJ is 21.5 g; these include small species, such as *Anolis trachyderma* and *Gonatodes concinnatus*, and large species, such as *Enyalioides cofanorum*, *E. laticeps*, and *Tropidurus umbra*. Likewise at NTL, *Anolis fuscoauratus* is the most abundant diurnal/arboreal species, but it accounts for only 1.4% of the total mass of lizards and 4.1% of the mass of diurnal/arboreal lizards there.

Most anurans and lizards are feeding generalists on a variety of arthropods. Although most frogs include ants in their diets, some species are ant-specialists. These include the diurnal/terrestrial dendrobatids, members of the *Bufo typhonius* complex, and some small leptodactylids, as well as the nocturnal/terrestrial microhylids. One species included here, *Physalaemus petersi*, feeds almost exclusively on termites; it is represented by 65 individuals (87 g, 8.1% of total anuran mass) at SJ but only one individual (1.4 g, 0.2% of total anuran mass) at NTL. Nine ant-specialists are present at SJ and NTL; they are represented by 33 and 72 specimens, respectively. These nine species account for 144.5 g (13.5% of total anuran mass) at SJ and 284.7 g (43.2% of total anuran mass) at NTL. The discrepancy mostly is owing to the fact that two of these species at NTL (*Bufo typhonius* "A" and *B. typhonius* "C") are the two most abundant species in our samples. By excluding the data on these two species at both sites, the difference in mass of ant-specialists is far more similar between the sites—13.8 g (1.3% of total anuran mass) at SJ and 26.8 g (4.1% of total anuran mass) at NTL.

Among the lizards found in the study zones, all are feeding generalists, except two diurnal/arboreal species, *Tropidurus plica* and *T. umbra*, which are ant-specialists. One *T. plica* was found at NTL; its mass of 81.0 g is 23.6% of the total lizard mass at that site. One *T. umbra* was found at each site; the individual from SJ had a mass of 15.5 g (4.1% of the total lizard mass), and the one from NTL had a mass of 16.5 g (4.8% of the total lizard mass).

Comparison with Other Regions

Although our collections from the sites in northern Loreto are far from complete, it is possible to make some meaningful comparisons with the herpetofaunas from other

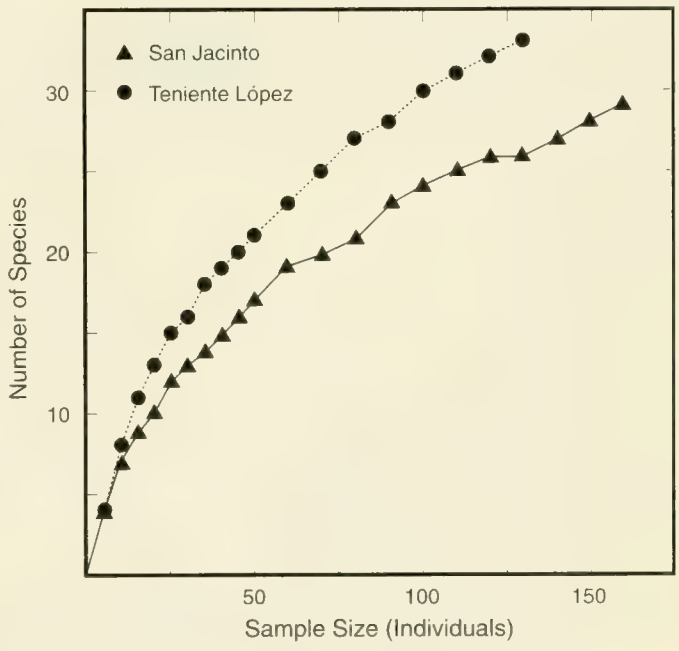


Fig. 23. Projected rarefaction curves for anurans based on species and their abundance at the study sites. The curve for lizards at both sites approximates the base of the curve for anurans at San Jacinto.

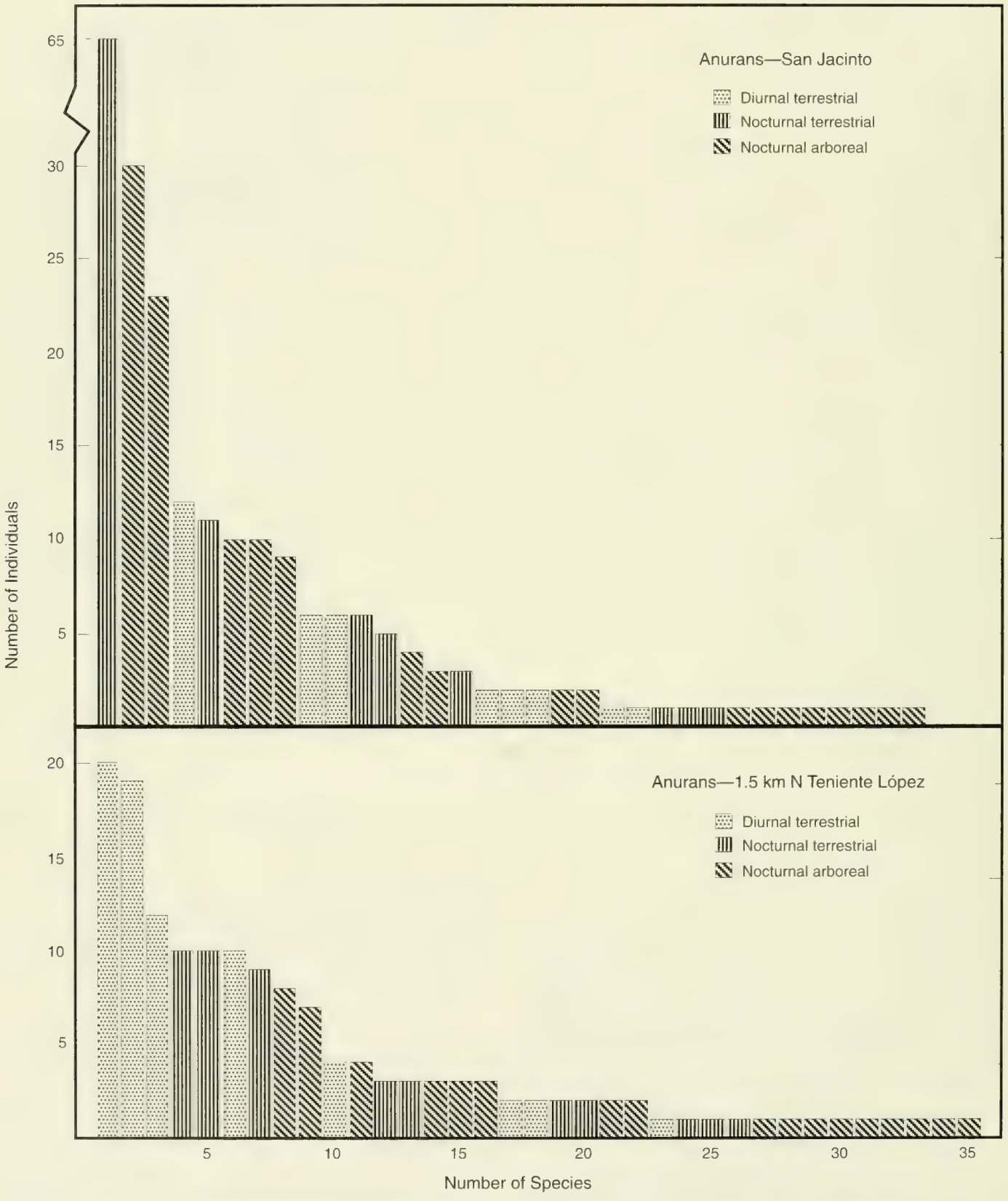


Fig. 24. Comparative abundance of anurans with respect to microhabitat in the study zones at San Jacinto and at 1.5 km N Teniente López. Each bar represents a different species.

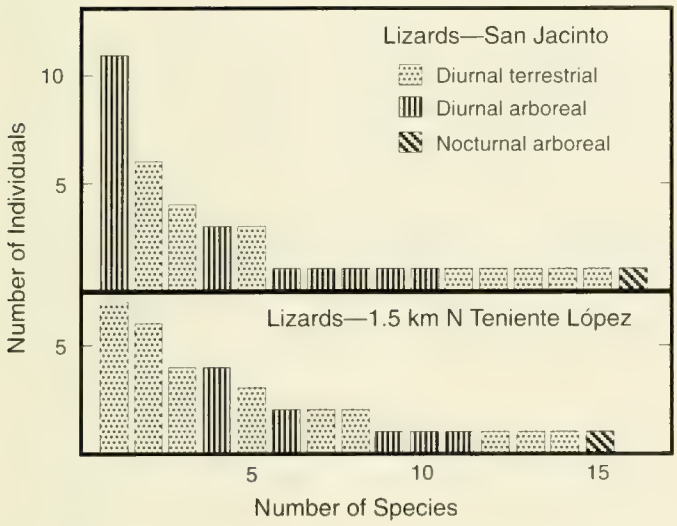


Fig. 25. Comparative abundance of lizards with respect to microhabitat in the study zones at San Jacinto and at 1.5 km N Teniente López. Each bar represents a different species.

sites in the upper and central Amazon Basin. The sites are:

Santa Cecilia, Ecuador.—A site at 340 m on the Río Aguarico (00°03' N, 76°59' W); aseasonal lowland tropical rainforest with a herpetofauna of 177 species (data updated from Duellman, 1978).

Cocha Cashu, Peru.—A site at 300–400 m on the Río Manu (11°54 S, 71°22' W); seasonal lowland tropical rainforest with a herpetofauna of 146 species (Rodríguez and Cadle, 1990).

Cuzco Amazónico, Peru.—A site at 220 m on the Río Madre de Díos (12°05' S, 69°05' W); seasonal lowland tropical rainforest with a herpetofauna of 145 species (Duellman and Salas, 1991).

Manaus, Brazil.—The Minimum Critical Size of Ecosystems study sites (02°20' S, 60°00' W), 70–90 km N Manaus; seasonal lowland tropical rainforest with a herpetofauna of 128 species (Zimmerman and Rodrigues, 1990).

As shown in Table 4, the similarities among anurans and lizards is high between northern Loreto and Santa Cecilia (CBRs = 0.67 and 0.68, respectively). These similarities are exceeded only by that of anurans (CBR = 0.71) between Cocha Cashu and Cuzco Amazónico and approximated by that of anurans (CBR = 0.63) between Cocha Cashu and Santa Cecilia and that of lizards (CBR = 0.61) between Cocha Cashu and Cuzco Amazónico. The similarities between Cocha Cashu and Cuzco Amazónico are expected because of their close proximity (260 km apart) in the same drainage system. Likewise, the northern Loreto sites are separated from Santa Cecilia by a distance of about 280 km, but they are in different drainage systems. With the exception of the low similarity of lizards (CBR = 0.38) between Cuzco Amazónico and northern Loreto, the similarities of both anurans and lizards are much lower (CBR = 0.33–0.42) between Manaus and all other sites. A distance factor may be significant here; Manaus is separated from all of the other sites by distances of more than 1500 km. In comparison with the other sites (all in the upper Amazon Basin), the herpetofauna at Manaus is depauperate. Moreover, similarity between Manaus and the upper Amazonian sites is exaggerated negatively by the presence at Manaus of several species (e.g., *Chiasmocleis shudikarensis*, *Pipa arrabali*, and *Leposoma guianense*) that are principally Guianan in distribution.

The intermediate geographic location of the sites in northern Loreto between Santa Cecilia to the north and Cocha Cashu and Cuzco Amazónico to the south is reflected in the composition of the herpetofauna. Many of the species occur at all of these sites in the upper Amazon Basin, but others reach either their northern or southern limits of distribution in Loreto. Those reaching their southern limits include *Hyla albopunctulata*, *Eleutherodactylus quaquaversus*, *Chiasmocleis bassleri*, *Anolis transversalis*, and *Enyalioides cofanorum*, whereas *Hyla koechlini*, and *Eleutherodactylus malkini* reach the northern limits of their distributions in the region.

Two species found at NTL have affinities with the Andean slopes. *Phyllomedusa hulli* is a member of the *Phyllomedusa buckleyi* group, which otherwise occurs on the slopes of Andes, the Cordillera de la Costa in northern Venezuela, and in Central America (Cannatella, 1980). Except for the record from NTL, *Alopoglossus copii* is known only from the Andean slopes of Ecuador (Ruibal, 1952; Peters and Donoso-Barros, 1970). Specimens assigned to that species from Santa Cecilia in the Amazon Basin in Ecuador (Duellman, 1978) have been reidentified as *A. angulatus*.

Two species that are widespread in the Amazon Basin, *Bufo marinus* and *Ameiva ameiva*, characteristically inhabit disturbed areas and clearings; they seldom venture far into closed forest. Their principal avenues of dispersal seem to be major rivers, which have broadly exposed banks during the dry season, and roads. *Bufo marinus* was present in the camp clearings at SJ and TL, but *Ameiva ameiva* was not observed at either site, nor was it observed along roads or at Andoas, which has extensive clearings along a major river, the Río Pastaza.

Table 3. Percentages of individuals and mass (in parentheses) of anurans and lizards with respect to diel activity and microhabitat in study zones at San Jacinto (SJ) and at 1.5 km N Teniente López (NTL).

	ANURANS				LIZARDS			
DIEL/MICROHABITAT	SJ		NTL		SJ		NTL	
Diurnal/terrestrial	14.2	(11.0)	45.8	(44.0)	47.4	(53.6)	72.2	(56.7)
Diurnal/arboreal	0.0	(0.0)	0.0	(0.0)	50.0	(40.2)	25.0	(35.7)
Nocturnal/terrestrial	41.2	(39.9)[1]	27.5	(29.8)	0.0	(0.0)	0.0	(0.0)
Nocturnal/arboreal	44.6	(49.1)	26.8	(26.2)	2.6	(6.1)	2.8	(7.6)

[1] Exclusive of *Bufo marinus*.

Table 4. Species of anurans and lizards in five regions in Amazonia. Abbreviations in headings to columns correspond to regions in first column. The upper number in each cell refers to anurans; the lower number refers to lizards. The number of species in each region is shown in boldface in the common cell; the numbers of species that are in common to two regions are in the upper right, and the coefficient of biogeographic resemblance is in italics in the lower left.

REGION	SC	NL	CC	CA	MA
Santa Cecilia, Ecuador (SC)	**81**	49	51	42	26
	30	18	16	16	9
Northern Loreto (NL)	*0.67*	**66**	37	33	21
	0.66	**24**	14	9	9
Cocha Cashu, Peru (CC)	*0.63*	*0.51*	**80**	51	21
	0.57	*0.56*	**26**	16	10
Cuzco Amazónico, Peru (CA)	*0.58*	*0.51*	*0.71*	**64**	20
	0.61	*0.38*	*0.65*	**23**	10
Manaus, Brazil (MA)	*0.42*	*0.39*	*0.34*	*0.38*	**42**
	0.33	*0.38*	*0.40*	*0.42*	**24**

LITERATURE CITED

AVILA-PIRES, T. C. S. 1995. Lizards of Brazilian Amazonia (Reptilia: Squamata). Zool. Verhand. 299:1–706.

AYARZAGÜENA, J., J. C. SEÑARIS, AND S. GORZULA. 1992. Un nuevo género para las especies del "grupo *Osteocephalus rodriguezi*" (Anura: Hylidae). Mem. Soc. Cien. Nat. 52:213–221.

BEEBE, W. 1944. Field notes on the lizards of Kartabo, British Guiana and Caripito, Venezuela. Part 2. Iguanidae. Zoologica 29:195–216.

BOULENGER, G. A. 1882. *Catalogue of the Batrachia Salientia s. Ecaudata in the Collection of the British Museum.* Ed. 2. London: Taylor and Francis.

BOULENGER, G. A. 1913. On a collection of batrachians and reptiles made by Dr. H. G. F. Spurrell, F. Z. S., in the Choco, Colombia. Proc. Zool. Soc. London 1913:1019–1038.

CALDWELL, J. P., AND C. W. MYERS. 1990. A new poison frog from Amazonian Brazil, with further revision of the *quinquevittatus* group of *Dendrobates*. Am. Mus. Novit. 2988:1–21.

CAMPBELL, J. A., AND W. W. LAMAR. 1989. *The Venomous Reptiles of Latin America.* Ithaca, New York: Comstock Publ. Assoc.

CANNATELLA, D. C. 1980. A review of the *Phyllomedusa buckleyi* group (Anura: Hylidae). Occas. Pap. Mus. Nat. Hist. Univ. Kansas 87:1–40.

COCHRAN, D. M., AND C. J. GOIN. 1970. Frogs of Colombia. Bull. U. S. Natl. Mus. 288:1-655.

COPE, E. D. 1874. On some Batrachia and Nematognathi brought from the upper Amazon by Prof. Orton. Proc. Acad. Nat. Sci. Philadelphia 25:120–137.

CRUMP, M. L. 1971. Quantitative analysis of the ecological distribution of a tropical herpetofauna. Occas. Pap. Mus. Nat. Hist. Univ. Kansas 3:1–62.

CRUMP, M. L. 1977. Intrapopulation and interspecific variation of "standard" morphological characters of four closely related South American salamanders (*Bolitoglossa*) with description of habitat preferences. Herpetologica 33:415–426.

CRUZ, C. A. G. DA. 1990. Sobre as relações intergenéricas de Phyllomedusinae da floresta Atlântica (Amphibia, Anura, Hylidae). Rev. Brasil. Biol. 50:7-9–726.

DE SÁ, R. O., AND L. TRUEB. 1991. Osteology, skeletal development, and chondrocranial structure of *Hamptophryne boliviana* (Anura: Microhylidae). J. Morphol. 209:311–330.

DIXON, J. R., AND P. SOINI. 1986. The reptiles of the upper Amazon Basin, Iquitos region, Peru. Milwaukee, Wisconsin: Milwaukee Public Museum.

DUELLMAN, W. E. 1970. Hylid frogs of Middle America. Monogr. Mus. Nat. Hist. Univ. Kansas 1:1–753.

DUELLMAN, W. E. 1973a. Frogs of the *Hyla geographica* group. Copeia 1973:515–533.

DUELLMAN, W. E. 1973b. Description of new lizards from the upper Amazon Basin. Herpetologica 29:228–231.

DUELLMAN, W. E. 1974. Taxonomic notes on *Phyllomedusa*(Anura: Hylidae) from the upper Amazon Basin. Herpetologica 30:105–112.

DUELLMAN, W. E. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. Misc. Publ. Mus. Nat. Hist. Univ. Kansas 65:1–352.

DUELLMAN, W. E. 1987. Lizards in an Amazonian rain forest community: resource utilization and abundance. Natl. Geog. Res 3:489–500.

DUELLMAN, W. E. 1988. Patterns of species diversity in anuran amphibians in the American tropics. Ann. Missouri Bot. Gard. 75:79–104.

DUELLMAN, W. E. 1989. Tropical herpetofaunal communities: patterns of community structure in neotropical forests. Pp 61–88 *in* M. L. Harmelin-Vivien and F. Bourlière (Eds.), *Vertebrates in Complex Tropical Systems.* New York: Springer Verlag.

DUELLMAN, W. E. 1990. Herpetofaunas in neotropical rainforests: comparative composition, history, and resource utilization. Pp. 455–505 *in* A. H. Gentry (Ed.), *Four neotropical rainforests.* New Haven: Yale University Press.

DUELLMAN, W. E. 1993. Amphibian species of the world: additions and corrections. Spec. Publ. Mus. Nat. Hist. Univ. Kansas 21:1–372.

DUELLMAN, W. E., AND M. L. CRUMP. 1974. Speciation in frogs of the *Hyla parviceps* group in the upper Amazon Basin. Occas. Pap. Mus. Nat. Hist. Univ. Kansas 23:1–40.

DUELLMAN, W. E., AND M. S. HOOGMOED. 1992. Some hylid frogs from the Guiana Highlands, northeastern South America: new species, distributional records, and a generic reallocation. Occas. Pap. Mus. Nat. Hist. Univ. Kansas 147:1–21.

DUELLMAN, W. E., AND J. E. KOECHLIN. 1991. The Reserva Cuzco Amazónico, Peru: biological investigations, conservation, and ecotourism. Occas. Pap. Mus. Nat. Hist. Univ. Kansas 142:1–38.

DUELLMAN, W. E., AND M. LIZANA. 1994. Biology of a sit-and-wait predator, the leptodactylid frog *Ceratophrys cornuta.* Herpetologica 50:51–64.

DUELLMAN, W. E., AND V. R. MORALES. 1990. Variation, distribution, and life history of *Edalorhina perezi* (Amphibia, Anura, Leptodactylidae). Stud. Neotrop. Fauna Environ. 25:19–30.

DUELLMAN, W. E., AND A. W. SALAS. 1991. Annotated checklist of the amphibians and reptiles of Cuzco Amazónico, Peru. Occas. Pap. Mus. Nat. Hist. Univ. Kansas 143:1–13.

DUELLMAN, W. E., AND J. E. SIMMONS. 1988. Two new species of dendrobatid frogs, genus *Colostethus,* from the Cordillera del Cóndor, Ecuador. Proc. Acad. Nat. Sci. Philadelphia 140:115–124/

DUELLMAN, W. E., AND L. TRUEB. 1989. Two new treefrogs of the *Hyla parviceps* group from the Amazon Basin in southern Peru. Herpetologica 45:1–10.

DUELLMAN, W. E., AND J. J. WIENS. 1993. Hylid frogs of the genus *Scinax* Wagler, 1830, in Amazonian Ecuador and Peru. Occas. Pap. Mus. Nat. Hist. Univ. Kansas 153:1–57.

FROST, D. R. 1985. *Amphibian Species of the World.* Lawrence, Kansas: Allen Press, Inc. and Assoc. Syst. Collect.

FROST, D. R. 1992. Phylogenetic analysis and taxonomy of the *Tropidurus* group of lizards (Iguania: Tropiduridae). Am. Mus. Novit. 3033:1–68.

FROST, D. R., AND R. E. ETHERIDGE. 1989. A phylogenetic analysis and taxonomy of iguanian lizards (Reptilia: Squamata). Misc. Publ. Mus. Nat. Hist. Univ. Kansas 81:1–65.

GENTRY, A. H. 1988. Changes in plant community diversity and floristic composition on geographical and environmental gradients. Ann. Missouri Bot. Garden 75:1–34.

GOSNER, K. L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. Herpetologica 16:183–190.

GREENE, H. W. 1988. Antipredator mechanisms in reptiles. Pp. 1–152 *in* C. Gans and R. B. Huey (eds.), *Biology of the Reptilia: Defense and Life History,* Vol. 18. New York: Alan R. Liss, Inc.

HADDAD, C. F. B., AND M. MARTINS. 1994. Four species of Brazilian poison frogs related ro *Epipedobates pictus* (Dendrobatidae): taxonomy and natural history observations. Herpetologica 50:282–295.

HENLE, K. 1992. Zur Amphibienfauna Perus nebst Beschriebung eines neuen *Eleutherodactylus* (Leptodactylidae). Bonn Zool. Beitr. 43:79–129.

HERO, J.-M. 1990. An illustrated key to tadpoles occurring in the central Amazon Basin. Amazoniana 11:201–262.

HEYER, W. R. 1973. Systematics of the marmoratus group of the frog genus *Leptodactylus* (Amphibia, Leptodactylidae). Contr.. Sci. Nat. Hist. Mus. Los Angeles Co. 251:1–50.

HEYER, W. R. 1988. On frog distribution patterns east of the Andes. Pp. 225–273 *in* P. E. Vanzolini and W. R. Heyer (eds.). *Proceedings of a Workshop on Neotropical Distribution Patterns.* Rio de Janeiro: Acad. Brasil. Cien.

HEYER, W. R. 1994. Variation within the *Leptodactylus podicipinus-wagneri* complex of frogs (Amphibia: Leptodactylidae). Smithsonian Contr. Biol. 546:1–124.

HÖDL, W. 1990. Reproductive diversity in Amazonian lowland frogs. Fortschr. Zool. 38:41–60.

HOOGMOED, M. S. 1986. Biosystematic studies of the *Bufo "typhonius"* group. A preliminary progress report. Pp. 147–150 *in* Z. Roček (ed.), *Studies in Herpetology.* Prague: Charles Univ.

HOOGMOED, M. S., D. M. BORGES, AND P. CASCON. 1994. Three new species of the genus *Adelophryne* (Amphibia: Anura: Leptodactylidae) from northeastern Brazil, with remarks on the other species of the genus. Zool. Meded. 68:271–300.

HOOGMOED, M. S., AND J. LESCURE. 1984. A new genus and two new species of minute leptodactylid frogs from northern South America, with comments upon *Phyzelaphryne* (Amphibia: Anura: Leptodactylidae). Zool. Meded. 58:85–115.

JUNGFER, K.-H., 1989. Pfeilgiftfrösche der Gattung *Epipedobates* mit rot granuliertem Rücken aus dem Oriente von Ecuador und Peru. Salamandra 25:81–98.

JUNGFER, K.-H., AND L. C. SCHIESARI. 1995. Description of a central Amazonian and Guianan tree frog, genus *Osteocephalus* (Anura, Hylidae), with oophagus tadpoles. Alytes 13:1–13.

KREBS, C. J. 1989. *Ecological Methodology.* New York: Harper Collins Publishers, Inc.

LESCURE, J.-L., AND J. P. GASC. 1986. Partage de l'espace forestier par les amphibiens et les reptiles en Amazonie du nord-ouest. Caldasia 15:707–723.

LÖTTERS, S. 1988. Redefinition von *Dendrobates quinquevittatus* (Steindachner, 1864) (Anura: Dendrobatidae). Salamandra 24:72–74.

LYNCH, J. D. 1976. The species groups of the South American frogs of the genus *Eleutherodactylus* (Leptodactylidae). Occas. Pap. Mus. Nat. Hist. Univ. Kansas 61:1–24.

LYNCH, J. D. 1980. A taxonomic and distributional synopsis of the Amazonian frogs of the genus *Eleutherodactylus*. Am. Mus. Novit. 2696:1–24.

LYNCH, J. D., AND W. E. DUELLMAN. 1980. The *Eleutherodactylus* of the Amazonian slopes of the Ecuadorian Andes (Anura: Leptodactylidae). Misc. Publ. Mus. Nat. Hist. Univ. Kansas 69:1–86.

LYNCH, J. D., AND W. E. DUELLMAN. 1995. A new fat little frog (Leptodactylidae: *Eleutherodactylus*) from the lofty Andean grasslands of southern Ecuador. Occas. Pap. Nat. Hist. Mus. Univ. Kansas 173:1–7.

MARTINS, M. 1991. The lizards of Balbina, Central Amazonia, Brazil: a qualitative analysis of resource utilization. Stud. Neotrop. Fauna Environ. 26:179–190.

MARTINS, M., AND A. J. CARDOSO. 1987. Novas espécies de hylídos do Estado do Acre (Amphibia: Anura). Rev. Brasil. Biol. 47:549–558.

MORALES, V. R. 1994. Taxonomía sobre algunos *Colostethus* (Anura: Dendrobatidae) de Sudamérica, con descripción de dos especies nuevas. Rev. Españoila Herpetol. 8:95–103.

MEEDE, U. 1980. Beobachtungen an *Dendrobates quinquevittatus* und *Phyllobates femoralis* (Amphibia: Salientia: Dendrobatidae). Salamandra 16:38–51.

MIYATA, K. 1985. A new *Lepidoblepharus* from the Pacific slope of the Ecuadorian Andes (Sauria: Gekkonidae). Herpetologica 41:121–127.

MYERS, C. W., AND J. E. CADLE. 1994. A new genus for South American snakes related to *Rhadinaea obtusa* (Colubridae) and resurrection of *Taeniophallus* Cope for the "*Rhadinaea*" *brevirostris* group. Am. Mus. Novit. 3102:1–33.

MYERS, C. W., AND W. E. DUELLMAN. 1982. A new species of *Hyla* from Cerro Colorado, and other tree frog records and geographical notes from western Panama. Am. Mus. Novit. 2752:1–32.

NELSON, C. E. 1975. Another new miniature 4-toed South American microhylid frog (*Syncope*). J. Herpetol. 9:81–84.

PETERS, J. A., AND R. DONOSO-BARROS. 1970. Catalogue of the Neotropical Squamata: Part II. Lizards and amphisbaenians. Bull. U. S. Natl. Mus. 297:1–293.

PETERS, J. A., AND B. OREJAS-MIRANDA. 1970. Catalogue of the Neotropical Squamata: Part I. Snakes. Bull. U. S. Natl. Mus. 297:1–347.

RODRÍGUEZ, L. O. 1992. Structure et organization du peuplement d'anoures de Cocha Cashu, Parc National Manu, Amazonie Péruvienne. Rev. Ecol. 47:151–197.

RODRÍGUEZ, L. O. AND J. E. CADLE. 1990. A preliminary overview of the herpetofauna of Cocha Cashu, Manu National Park, Peru. Pp. 410–425 *in* A. H. Gentry (Ed.), *Four neotropical rainforests*. New Haven: Yale University Press.

RODRÍGUEZ, L. O., AND W. E. DUELLMAN. 1994. Guide to the frogs of the Iquitos region, Amazonian Peru. Spec. Publ. Nat. Hist. Mus. Univ. Kansas 22:1–80.

RUIBAL, R. 1952. Revisionary studies of some South American Teiidae. Bull. Mus. Comp. Zool. 106:477–529.

RUÍZ-CARRANZA, P. M., J. I. HERNÁNDEZ-CAMACHO, AND J. V. RUEDA-ALMONACID. 1988. Una nueva especies de *Phyllomedusa* Wagler 1830 (Amphibia: Anura: Hylidae) del noroeste de Colombia. Trianea 2:372–383.

SAVAGE, J. M., AND W. R. HEYER. 1967. Variation and distribution in the tree-frog genus *Phyllomedusa* in Costa Rica, Central America. Beitr. Neotrop. Fauna 5:111–131.

SCHLÜTER, A. 1984. Ökologische Untersuchunger an einem Stillgewasser im tropischen Regelwald von Peru unter besonderer Berucksichtigung der Amphibien. Doct. Dissertation, Univ. Hamburg.

SCHULTE, R. 1987. Der Erstnachweis von *Dendrobates zaparo* (Silverstone, 1976) für Peru (Amphibia; Salientia; Dendrobatidae). Sauria 9:17–18.

SCHULTE, R. 1989. Nueva especie de rana venenosa del género *Epipedobates* registrada en la Cordillera Oriental, Departamento de San Martín. Bol. Lima 63:41–46.

SILVA, N. G. DA. 1993. The snakes from Samuel Hydroelectric Plant and vicinity, Rondônia, Brazil. Herpetol. Nat. Hist. 1:37–86.

SILVERSTONE, P. A. 1976. A revision of the poison-arrow frogs of the genus *Phyllobates* Bibron *in* Sagra (Family Dendrobatidae). Sci. Bull. Nat. Hist. Mus. Los Angeles Co. 27:1–53.

SOKAL, R. R., AND J. R. ROHLF. 1981. *Biometry*. 2nd Ed. New York: W. H. Freeman.

TOFT, C. A., AND W. E. DUELLMAN. 1979. Anurans of the lower Río Llullapichis, Amazonian Peru: a preliminary analysis of community structure. Herpetologica 35:71–77.

TRUEB, L., AND W. E. DUELLMAN. 1971. A synopsis of neotropical hylid frogs, genus *Osteocephalus*. Occas. Pap. Mus. Nat. Hist. Univ. Kansas 1:1–47.

UZZELL, T., AND J. C. BARRY. 1971. *Leposoma percarinatum*, a unisexual species related to *L. guianense;* and *Leposoma ioanna*, a new species from Pacific coastal Colombia (Sauria: Teiidae). Postilla 154:1–39.

VANZOLINI, P. E. 1986. Addenda and corrigenda to the catalogue of neotropical squamata. Smithsonian Herpetol. Info. Serv. 70:1–25.

VANZOLINI, P. E., AND E. E. WILLIAMS. 1970. South American anoles: the geographic differentiation and evolution of the *Anolis chrysolepis* species group (Sauria, Iguanidae). Arq. Zool. Univ. São Paulo 19:1–298.

WALKER, C. F. 1973. A new genus and species of microhylid frog from Ecuador. Occas. Pap. Mus. Nat. Hist. Univ. Kansas 20:1–7.

ZIMMERMAN, B. 1983. A comparison of structural features of calls of open and forest habitat frogs species in the central Amazon. Herpetologica 39:235–246.

ZIMMERMAN, B., AND J. P. BOGART. 1984. Vocalizations of primary forest frog species in the central Amazon. Acta Amazonica 14:473–519.

ZIMMERMAN, B., AND M. T. RODRIGUES. 1990. Frogs, snakes, and lizards of the INPA-WWF reserves near Manaus, Brazil. Pp. 426–454 *in* A. H. Gentry (ed.), *Four Neotropical Rainforests*. New Haven: Yale Univ. Press.

ZWEIFEL, R. G. 1986. A new genus and species of microhylid frog from the Cerro de la Neblina region of Venezuela and a discussion of relationships among New World microhylid genera. Am. Mus. Novit. 2863:1–24.

ANNOUNCEMENT

The *University of Kansas Science Bulletin* (continuation of the *Kansas University Quarterly*) is an outlet for scholarly scientific investigations carried out at the University of Kansas or by University faculty and students. Since its inception, volumes of the *Bulletin* have been variously issued as single bound volumes, as two or three multi-paper parts or as series of individual papers. Issuance is at irregular intervals, with each volume prior to volume 50 approximately 1000 pages in length. Effective with volume 50, page size has been enlarged, reducing the length of each volume to about 750 pages.

The supply of all volumes of the *Kansas University Quarterly* is now exhausted. However, most volumes of the *University of Kansas Science Bulletin* are still available and are offered, in exchange for similar publications, to learned societies, colleges and universities and other institutions, or may be purchased at $30.00 per volume. Where some of these volumes were issued in parts, individual parts are priced at the rate of 3 cents per page. Current policy, initiated with volume 46, is to issue individual papers as published. Such separata may be purchased individually at the rate of 7 cents per page, with a minimum charge of $1.50 per separate. Subscriptions for forthcoming volumes may be entered at the rate of $30.00 per volume. All communications regarding exchanges, sales and subscriptions should be addressed to the EXCHANGE LIBRARIAN, UNIVERSITY OF KANSAS LIBRARIES, LAWRENCE, KANSAS 66045.

Reprints of individual papers for personal use by investigators are available for most recent and many older issues of the *Bulletin*. Such requests should be directed to the author.

The International Standard Serial Number of this publication is US ISSN 0022-8850.

Editor
Charles D. Michener

Editorial Board
Meredith Lane, *Chairman*
James S. Ashe
George W. Byers
Christopher Haufler
Norman A. Slade

THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. 55, No. 11, pp. 377-424 September 30, 1995

OCT 13 1995

Phylogenetic Studies of the Families of Short-Tongued Bees (Hymenoptera: Apoidea)[1]

Byron A. Alexander[2] and Charles D. Michener[2]

TABLE OF CONTENTS

Abstract 378
Introduction 378
Materials 379
Characters 379
List of Characters and Codes for Their States 381
Characters for Series I Analyses 381
Characters for Series II Analyses 387
The Two Series of Analyses 388
Methods of Analysis 388
Computer Programs 388
Character Weighting 389
Character Polarization 389
Results 389
Monophyly of Bees 390
Series I, Part 1: Analyses Using Exemplars 390
Equal Weighting 390
Successive Approximations Weighting 390
Implied Weighting 395
Series I, Part 2: Analyses Based on Family Groundplans 399
EQWT Groundplans 399
IW Groundplans 403
Series II, Part 1: Analyses Using Exemplars 403
Equal Weighting 403
Successive Approximations Weighting 404
Implied Weighting 409
Series II, Part 2: Analyses Based on Family Groundplans 409
I-226 Groundplan 413
I-336 Groundplan 413
Discussion 413
General 413
Colletidae 415
Stenotritidae 416
Andrenidae (and Oxaeidae) 417
Halictidae 417
Melittidae + L-T Bees 418
Relationships Among S-T Bee Families 418
Biogeography and Fossil Bees 419
Comments on Bee Classification 420
Literature Cited 423

[1]Contribution number 3146 from the Snow Entomological Museum, Natural History Museum, and the Department of Entomology, University of Kansas.

[2]Snow Entomological Museum, Snow Hall, University of Kansas, Lawrence, Kansas 66045, U.S.A.

ABSTRACT

Phylogenetic analyses of short-tongued bees were made using species representing 48 taxa of short-tongued bees (plus 9 taxa of long-tongued bees and 8 of spheciform wasps) and 109 or 114 characters of adult morphology. Two series of analyses compared the phylogenetic implications of two competing hypotheses of character evolution for the glossa. In each series, analyses were made using exemplars and family groundplans reconstructed from the results of the exemplar analyses. The effects of various character weighting procedures were also compared.

The monophyly of bees is strongly supported. Although several features of the colletid glossa are clearly apomorphic, our analyses do not support the hypothesis that the shape of the glossa was pointed in the ancestral bee, because Colletidae whose males have a pointed glossa are not located near the base of colletid or bee phylogeny. Families found to be monophyletic are Andrenidae (including Oxaeinae), Halictidae, Stenotritidae (represented in these analyses by only one species), and probably Colletidae. Melittidae are clearly paraphyletic, and are the group of short-tongued bees from which long-tongued bees arose. The Melittidae is subdivided into three families, the Meganomiidae, Dasypodidae, and Melittidae proper.

Several conflicting hypotheses of relationships among these families are supported in the various analyses, and these hypotheses are highly sensitive to character weighting and assumptions about polarity or ordering of transformation series for only a handful of characters. Although the groundplan analyses provide better resolution than the exemplar analyses, the characters that provide this resolution are highly variable within all the major families.

The biogeography and fossil record of bees are briefly discussed in the light of these analyses.

INTRODUCTION

This is the sequel to Roig-Alsina and Michener's (1993) account of the phylogeny and classification of long-tongued bees. As noted in that paper, the classification and the phylogenetic hypotheses for bees have never reached a stage where most authors can agree on one classification and one probable phylogeny. The objective of this paper, therefore, is to contribute to a solution of the phylogenetic and classificatory problems among bees, with a primary focus on taxa that have commonly been assigned the rank of family. Our results, however, are indecisive in various respects; differences of opinion will continue.

The short-tongued (S-T) bees include the forms commonly placed in the families Andrenidae, Colletidae, Halictidae, Melittidae, Oxaeidae, and Stenotritidae. They seem structurally more diverse than the long-tongued (L-T) bees. They lack various synapomorphies of L-T bees. For example, (1) the first two segments (or at least the second segment) of the labial palpus are not elongate and flattened with the third and fourth minute; these are features of L-T bees. (2) The stipital comb and its concavity, found in most L-T bees, are absent (except for one melittid, *Eremaphanta*). (3) The galeal comb is present, at least in some members of every major group; it is lost or nearly so in L-T bees. As should be expected of a group defined by plesiomorphies, the S-T bees are paraphyletic, L-T bees having arisen monophyletically from among them (Roig-Alsina and Michener, 1993).

We refer readers to Roig-Alsina and Michener (1993) for a brief account of the L-T bees that have lost their long tongues and S-T bees that have developed long tongues independently from those of L-T bees. The same authors gave a brief account of aspects of the history of bee classification. Repetition of this material here is unnecessary.

Since various abbreviations are introduced at different points through this paper, they are listed here for ready reference.

ci — consistency index (Kluge and Farris, 1969)
EQWT — equal weight groundplan
H86 — Hennig86 (computer program by Farris, 1988)
IW — implied weight
L — length of a tree, measured in number of steps
L-T — long-tongued
MCL-T — the Melittidae + *Ctenoplectra* + long-tongued bee clade
MMD — Michener, McGinley, and Danforth, 1994
NA — nonadditive (= unordered)
NONA — No Name (computer program by Goloboff, 1993a)
PAUP — Phylogenetic Analysis Using Parsimony (computer program by Swofford, 1993)
R-AM — Roig-Alsina and Michener, 1993
ri — retention index (Farris, 1989a, b)
S-T — short-tongued
S1, S2, etc. — first, second, etc., metasomal sternum
T1, T2, etc. — first, second, etc., metasomal tergum

MATERIALS

Our analyses are based on morphological studies of adults. The 65 taxa (48 S-T bees, 9 L-T bees, 8 spheciform wasps) were selected to represent all families, subfamilies and tribes of S-T bees and representatives of the L-T bees and of the spheciform wasps (Table 1). We use the term "spheciform wasps" for the basal, nonbee lineages in the superfamily Apoidea as delineated in recent cladistic analyses by Alexander (1992a) and Brothers and Carpenter (1993). Many authors (e.g., Evans, 1959; Bohart and Menke, 1976) assign all these wasps to one family called Sphecidae, whereas many other authors (e.g., Krombein, 1979; Finnamore, 1993) prefer to recognize several families; our aim is to use an unambiguous descriptor for these wasps without advocating a particular taxonomic rank for them. More than one representative of a subfamily or tribe was included in the study in cases where there is considerable diversity within the subfamily or tribe, or where there is some doubt as to the positions of certain taxa. We believe that the representatives selected provide a good sample of the diversity among S-T bees, even though only 48 species represent perhaps 10,000 species of S-T bees.

The species listed in Table 1 are exemplars of genera or groups of genera. In our account we often refer to characters of a genus; in reality we mean of the particular species listed in Table 1. When we refer to characters of a family-group taxon, we mean that taxon as represented by the species listed in Table 1, unless otherwise stated. Most of the characters used no doubt vary little within any one genus, although we do know of cases where one of our characters varies among species of a genus. An example is character 84, number of submarginal cells. In various genera such as *Leioproctus* and *Andrena,* the number varies among subgenera or among species of a subgenus, although among other taxa this character is often phylogenetically informative at tribal to familial levels.

CHARACTERS

As will be explained in more detail below (see The Two Series of Analyses), our study involved two sets of analyses designed to examine the phylogenetic implications of two competing hypotheses about the evolution of the glossa of bees. Our first series of analyses (Series I) made use of 109 characters, 53 of which had more than two states. A second series of analyses (Series II) partitioned three characters from Series I into two or more characters. Series II had 114 characters in all, of which 53 had more than two states. In searching for characters, we looked for morphological features with two or more discrete states that could be clearly defined and delineated. Our search started with the list of characters used by Roig-Alsina and Michener (1993) in their study of L-T bees. Some such characters were found to be useful in unmodified form for S-T bees, but for other characters the relevant states were different from those used in the study of L-T bees. We added many characters as a result of comparing S-T bees with one another and especially with spheciform wasps. Because characters were polarized by a simultaneous analysis of the ingroup (57 species of bees) and the outgroup (8 species of spheciform wasps), a few characters were included that do not vary among S-T bees but help to resolve relationships among taxa in the outgroup or in L-T bees.

With the exception of three glossal characters in Series II, which were specially coded in order to reflect a specific hypothesis about the evolution of the glossa of bees, structures that look the same always received the same state code. Thus, if a given structure exists in, for example, a wasp and a megachilid, it received the same character state code. To give separate codes in such a case would imply *a priori* phylogenetic knowledge. In a parsimony analysis, assigning the same character state to a similar-looking structure in two taxa is an implicit hypothesis that the structures are homologous. Even though we knew that certain states given the same coding could not be homologous, because this would be inconsistent with codings used for other characters, the purpose of a parsimony analysis is to reconcile these conflicting hypotheses of homology (Sober, 1988).

An infinity of characters could be expected, representing differences among the species listed in Table 1. We have preferred characters that, by examination of our exemplar taxa as well as experience with other taxa not formally included within this study, vary at genus, tribal or higher levels. Thus a multitude of characters such as hair color, punctation, and other surface sculpturing have not been included in our study because they appear to diverge and converge repeatedly in all sorts of combinations. Recognizing homologies in a taxonomically broad study such as this one is probably impossible for such characters, although in a restricted study, for example of species within one genus, the same characters might well be useful.

We think it is quite possible to bias a phylogenetic analysis inadvertently to produce a hypothesis supporting a prior classification. This is because one would normally include in an analysis all those characters known to distinguish established taxa, whereas one might or might not notice and include characters that could produce an entirely new arrangement of the taxa. Our principal defense against such biasing is that we included many potentially informative characters and also that we used characters that distinguish established taxa in one group or family but vary widely within established taxa in other parts of the study, where they could demonstrate new phylogenetic arrangements if the established taxa are weakly supported.

Specimens of nearly all species in Table 1 were treated with 10% KOH (room temperature, often for

Table 1. LIST OF TAXA USED AS EXEMPLARS.
Arranged according to recently accepted families and subfamilies.
(See Discussion for assessment of higher categories.)
The numbers are those used in Table 2.

S-T BEES

COLLETIDAE
- Colletinae
  - 1 *Colletes inaequalis* Say
  - 16 *Mourecotelles mixta* Toro & Cabezas
  - 3 *Leioproctus delahozi* Toro
  - 7 *Lonchopria zonalis* Reed
  - 4 *Callomelitta antipodes* (Smith)
  - 5 *Scrapter heterodoxus* (Cockerell)
  - 8 *Eulonchopria punctatissima* Michener
  - 6 *Trichocolletes venustus* (Smith)
- Diphaglossinae
  - 2 *Caupolicana ruficollis* Friese
  - 17 *Diphaglossa gayi* Spinola
  - 19 *Crawfordapis luctuosa* (Smith)
  - 20 *Mydrosoma serratum* (Friese)
  - 9 *Cadeguala occidentalis* (Haliday)
- Hylaeinae
  - 12 *Hyleoides concinna* (Fabricius)
  - 11 *Hylaeus basalis* (Smith)
  - 13 *Amphylaeus morosus* (Smith)
  - 18 *Meroglossa impressifrons* (Smith)
- Euryglossinae
  - 10 *Euryglossa subsericea* Cockerell
  - 15 *Euryglossula chalcosoma* (Cockerell)
- Xeromelissinae
  - 14 *Chilicola vernalis* (Philippi)

STENOTRITIDAE
- 21 *Ctenocolletes smaragdinus* (Smith)

ANDRENIDAE
- Andreninae
  - 22 *Andrena erythrogaster* (Ashmead)
  - 27 *Megandrena enceliae* (Cockerell)
  - 26 *Euherbstia excellens* Friese
  - 28 *Alocandrena porteri* Michener
- Panurginae
  - 23 *Protandrena mexicanorum* (Cockerell)
  - 24 *Calliopsis subalpina* (Cockerell)*
  - 25 *Heterosarus albitarsus* (Cresson)**

OXAEIDAE
- 29 *Protoxaea gloriosa* (Fox)

HALICTIDAE
- Nomiinae
  - 30 *Dieunomia triangulifera* (Vachal)
  - 31 *Nomia melanderi* Cockerell
- Rophitinae
  - 32 *Dufourea marginata* (Cresson)
  - 33 *Systropha curvicornis* (Scopoli)
  - 47 *Xeralictus timberlakei* Cockerell
  - 41 *Conanthalictus nigricans* Timberlake
- Halictinae
  - 34 *Corynura chloris* (Spinola)
  - 35 *Pseudaugochlora graminea* (Fabricius)
  - 36 *Augochlora pura* (Say)
  - 37 *Halictus rubicundus* (Christ)
  - 39 *Agapostemon texanus* Cresson
  - 40 *Sphecodes gibbus* (Linnaeus)
  - 38 *Nomioides minutissima* (Rossi)

MELITTIDAE
- 42 *Meganomia gigas* Michener
- 43 *Macropis steironematis* Robertson
- 44 *Hesperapis carinata* Stevens
- 45 *Dasypoda panzeri* Spinola
- 46 *Melitta leporina* (Panzer)
- 56 *Haplomelitta ogilviei* (Cockerell)

L-T BEES

MEGACHILIDAE
- Fideliinae
  - 57 *Fidelia villosa* Brauns
  - 49 *Neofidelia profuga* Moure & Michener
  - 50 *Pararhophites orobinus* (Morawitz)
- Megachilinae
  - 51 *Lithurge apicalis* Cresson

APIDAE
- Apinae
  - 48 *Ctenoplectra fuscipes* (Friese)
  - 52 *Exomalopsis jenseni* Friese
- Xylocopinae
  - 53 *Manuelia gayi* (Spinola)
- Nomadinae
  - 54 *Nomada (Centrias)* sp., Kansas
  - 55 *Triepeolus distinctus* (Cresson)

SPHECIFORM WASPS

- 58 *Aphilanthops frigidus* (Smith)
- 59 *Philanthus multimaculatus* Cameron
- 60 *Passaloecus cuspidatus* Smith
- 61 *Tachytes distinctus* Smith
- 62 *Sphecius speciosus* (Drury)
- 64 *Astata bakeri* Parker
- 63 *Sphex ichneumoneus* (Linnaeus)
- 65 *Sceliphron caementarium* (Drury)

* This is shown as *Hypomacrotera* on the cladograms and Table 2; *Hypomacrotera* is variously regarded as a distinct genus or as a subgenus of *Calliopsis*.

** This is shown as *Pterosarus* on the cladograms and Table 2; *Pterosarus* is regarded as a subgenus of *Heterosarus* or as a distinct genus.

several days) and dismembered to expose internal skeletal structures. The material was examined and stored in glycerin.

LIST OF CHARACTERS AND CODES FOR THEIR STATES

Many annotations in the following list briefly describe the distribution of character states among taxa. Characters for which all outgroup taxa examined have a single state, state (0), are annotated: "State (0) characterizes the outgroup." Polarization of such characters is unproblematic. Other characters are annotated: "This character is variable within the outgroup," with additional explanation as necessary. Polarization of such characters is discussed in the section on methods of analysis.

As a rough check for character states that might be special synapomorphies of spheciform wasps, *Anoplius* (Pompilidae) and *Tiphia* (Tiphiidae) were examined in detail relative to the characters listed here, although they were not included in the data matrix. These genera are two readily available exemplars of the Vespoidea, which is the sister group of Apoidea (Brothers and Carpenter, 1993). For characters whose ancestral state is recognized, when no statement is made about *Anoplius* and *Tiphia* below, those genera and all the examined spheciform wasps except as indicated agree with state (0).

The abbreviation "[NA]" in the following list signifies that the character was treated as nonadditive (= "unordered" in PAUP) in the parsimony analyses. Multiple state characters for which a clear and unambiguous morphocline could not be hypothesized *a priori* were treated as nonadditive; all other multistate characters were additive (= ordered). (For characters with only two states, it makes no difference whether they are additive or nonadditive.) Other abbreviations used in the following list are: MMD = Michener, McGinley, and Danforth (1994); R-AM = Roig-Alsina and Michener (1993).

CHARACTERS FOR SERIES I ANALYSES

1. Hairs: (0) All simple. (1) Some of them branched or plumose. State (0) characterizes the outgroup; all bees are coded (1).

2. First flagellar segment of female: (0) Parallel sided or uniformly tapering toward base. (1) Capitate, i.e., long and slender basally and enlarged near apex to diameter of second segment as in *Caupolicana* and *Protoxaea* (Michener, 1944, fig. 17). State (0) characterizes the outgroup.

3. [NA] Upper end of subantennal suture (outer suture if there are two): (0) Directed toward lower margin of antennal socket (MMD fig. 180), sometimes divided (Y-shaped) below socket. (1) Directed toward outer margin of socket (MMD fig. 184). (2) Directed toward inner margin of socket (MMD figs. 81, 135). (3) Absent. When the suture is Y-shaped, the outer branch is directed toward the outer margin of the socket but the lower, undivided stem is directed toward the lower margin, and the code (0) is used. We use the code "?" when the antennal base is adjacent to the upper clypeal margin so that there is no space for the subantennal suture. This character varies within most major taxa including spheciform wasps, in which the "sutures" are sometimes evanescent lines even though traceable, rather than distinct sutures.

The weakness of the subantennal suture in spheciform wasps is related to lack of connection to a fan-shaped sheet of the tentorium (character 6), such as is found in bees.

4. [NA] Inner subantennal suture: (0) Absent, so that there is only one subantennal suture on each side, or none. (1) Present, meeting or closely approaching outer subantennal suture at upper margin of clypeus, so that subantennal area is pointed below. (2) Present and widely separated from outer subantennal suture, meeting upper margin of clypeus mesal to outer suture (MMD fig. 82). State (0) characterizes the outgroup as well as most bees.

5. Anterior tentorial pit: (0) High on epistomal suture (Michener, 1944, fig. 1; Eickwort, 1969, fig. 114). (1) Near or below middle of lateral part of epistomal suture. This character is closely connected with clypeal shape. Forms having state (1) necessarily have a clypeus extending well up on the front of the head, so that the lateral parts of the epistomal suture are steeply sloping. It is then possible for the tentorial pits to descend to low positions, i.e., state (1). Most spheciform wasps have state (0), and Brothers and Carpenter (1993) consider a low clypeus with the epistomal suture nearly horizontal as ancestral for aculeate Hymenoptera. State (1) is incompatible with such a clypeus.

6. Subantennal suture (outer subantennal suture if inner one is present): (0) Not connected to tentorium. (1) Connected more or less throughout length of suture to fan-shaped sheet of anterior end of tentorium. We have coded as (0) cases where the subantennal suture is absent. State (1) characterizes all bees. State (0) characterizes the outgroup. Many other aculeates lack subantennal sutures but they are present as state (1) in *Vespula,* no doubt convergent with the apoid condition.

The inner subantennal suture is also connected to a fan-like sheet of the tentorium in *Protandrena* and *Ctenocolletes.*

7. [NA] Integument of upper paraocular area of female: (0) Not differentiated from more median part of frons. (1) Area bordering eye with punctures sparser and smaller than on rest of frons, paler or darker in cleared specimens, margins usually diffuse. (2) Such an area broad, ovoid, with sharp limits, usually with scattered hairs, the area commonly called a facial fovea. (3) Fovea as in (2) but velvety with short hairs (MMD fig. 82). (4) Fovea a narrow groove, smooth and bare (as in *Hylaeus*). (5) Fovea narrow, with hairs. It is reasonable to suppose that state (0) is ancestral for aculeate Hymenoptera; facial foveae are absent in *Anoplius* and *Tiphia.* However, foveae are present in some spheciform wasps (Philanthinae, Crabroninae). Schuberth and Schönitzer (1993) have provided an account of the distribution and morphology of facial foveae and related structures in spheciform wasps and bees.

Lateral areas on T2 commonly vary in parallel with facial foveae. For this reason and because they are often hard to visualize (for example, a black area recognizable only if background is paler), the foveae on T2 are not used in the present analysis.

8. Lower lateral part of clypeus: (0) Not bent backward or only gently curved backward. (1) Bent back about 45^0 relative to median part of clypeus (Eickwort, 1969, fig. 78). (2) Strongly bent back, so that lateral parts are at angle of about 90^0 to median part (Michener, 1944, fig. 6). State (0) characterizes the outgroup.

9. Labrum: (0) Thin, retracted behind clypeal margin, supported by membrane behind lower part of clypeus. (1) Thick at least basally and hinged near lower margin of clypeus. State (0) characterizes the outgroup. All bees have state (1).

10. Lateral parts of labrum: (0) Not bent backward. (1)

Bent back less than 45°. (2) Bent back over 45°, sometimes nearly to 90° relative to the median part of the labrum. State (0) characterizes the outgroup. Although states (0) and (2) are very different, there are all intergradations between the states and assignment of a state was sometimes arbitrary.

11. Labrum of female: (0) Broader than long (not considering midapical process, such as is found in many Halictinae). (1) About as broad as long. (2) Longer than broad. State (0) is widespread in the outgroup as well as in other Aculeata such as *Anoplius* and *Tiphia,* and is no doubt ancestral for bees. When the labrum in outgroup taxa is about as long as broad, state (1), as in the spheciform wasp *Passaloecus,* it does not appear to be elongated in the same way as in some bees.

12. [NA] Anterior surface of labrum of female: (0) Flat, hairless or nearly so. (1) Entirely punctate and hairy except for narrow bare basal articulatory margin which is not elevated and presumably is not homologous to bare elevated area of state (3). (2) Largely bare and elevated, but with narrow, depressed, hairy apical margin. (3) With basal, largely bare, elevated area, clearly delimited from substantial, often punctate and hairy distal area which is sometimes produced as an apical process (Eickwort, 1969, figs. 7, 8). (The elevated basal area is sometimes called the labral process in *Andrena.*) Except for one of the spheciform wasps *(Tachytes)* that has a hairy labral margin, all have state (0), which is therefore regarded as ancestral. In *Tachytes,* although the labral margin is hairy so that we coded it as (2), the structure is on an otherwise typical thin, flat, spheciform labrum and does not closely resemble that of bees coded as (2).

13. Distal part of labrum of female: (0) Without marginal bristles although often hairy. (1) With marginal bristles which are simple and tapering, except sometimes branched in *Andrena.* This character is variable within the outgroup.

14. Distal part of labrum of female: (0) Not keeled. (1) Ending in a process with a strong, laterally compressed keel (Eickwort, 1969, figs. 7, 8). State (0) characterizes the outgroup. State (1) is found only in Halictidae.

15. Postoccipital pouch below foramen magnum: (0) Absent (R-AM fig. 11). (1) Shallow. (2) Distinct and deep (R-AM fig. 12). State (0) characterizes the outgroup. The pouch occurs in some of the taxa that have a long lobe consisting of the mentum and lorum projecting behind the labiomaxillary tube. When the proboscis is retracted, this lobe turns upward and occupies the pouch.

16. [NA] Apex of mandible of female: (0) With preapical tooth (apex of pollex) on upper margin. (1) With two preapical teeth on upper margin. (2) Simple, without tooth. This character is variable within the outgroup and among other Aculeata.

17. Arm of secondary tentorial bridge or equivalent: (0) Absent or completely fused to anterior tentorial arm, extending with the latter toward anterior tentorial pit (Fig. 3). (1) Crossing anterior tentorial arm near face and reaching face at antennal base, well above anterior tentorial pit; only small fanlike sheet or none between anterior parts of arms (Fig. 2). (2) Crossing anterior tentorial arm in middle part of head, well behind face, with a broad fanlike sheet occupying space between anterior parts of arms; arm of secondary tentorial bridge reaching face at antennal base, as in (1) (Fig. 1). State (0) characterizes the outgroup.

18. [NA] Attachment of secondary tentorial bridge to posterior wall of head (below foramen magnum): (0) Above and separate from hypostoma at posterior end of proboscidial fossa, but connected to hypostoma by vertical septum usually manifest externally as vertical black line extending upward from posterior end of proboscidial fossa (R-AM fig. 11). (1) As in (0) but vertical line wider, clear, representing thicker septum. (2) Secondary bridge fused directly to hypostoma posteriorly, thus eliminating vertical black line, fusion evident externally in that lines of attachment of bridge to head wall reach hypostoma independently at upper end of proboscidial fossa (R-AM fig. 12). (3) Close above hypostoma, seemingly fused to hypostoma a short distance anteriorly, vertical black line present but short, often visible on both surfaces of crest extending behind head above posterior end of proboscidial fossa, interior of crest being divided by the septum. This character varies within various major taxa including the outgroup.

19. Wall of proboscidial fossa fused to tentorium: (0) Not at all or only near posterior wall of head (Fig. 2; Michener, 1944, figs. 113, 115). (1) Forward to middle part of head (Fig. 1; Michener, 1944, figs. 8, 116). (2) Forward almost to clypeus (Fig. 3; Michener, 1944, fig. 114). State (0) characterizes the outgroup.

20. Posterior end of proboscidial fossa: (0) Closed, not opening onto posterior surface of head. (1) Open, i.e., posterior margin distinctly arched medially so that fossa opens onto posterior surface of head. State (0) characterizes the outgroup. State (1) is found in bees except for a few forms with the lower part of the head (clypeus, malar space, etc.) elongated so that the hypostomal region slants steeply upward posteriorly. This conformation eliminates the contrast between the more horizontal hypostomal region of most bees and the arched posterior margin of the fossa, so that this character is coded as (0). Except for such bees, state (0) of this character is probably related to the broad, shallow proboscidial fossa with lateral margins converging strongly posteriorly (for example, at right angles to one another in *Aphilanthops*) and the positions of the cardines that converge strongly toward their apices and have widely separated bases. These are all features that, with some variability, characterize spheciform wasps and not bees.

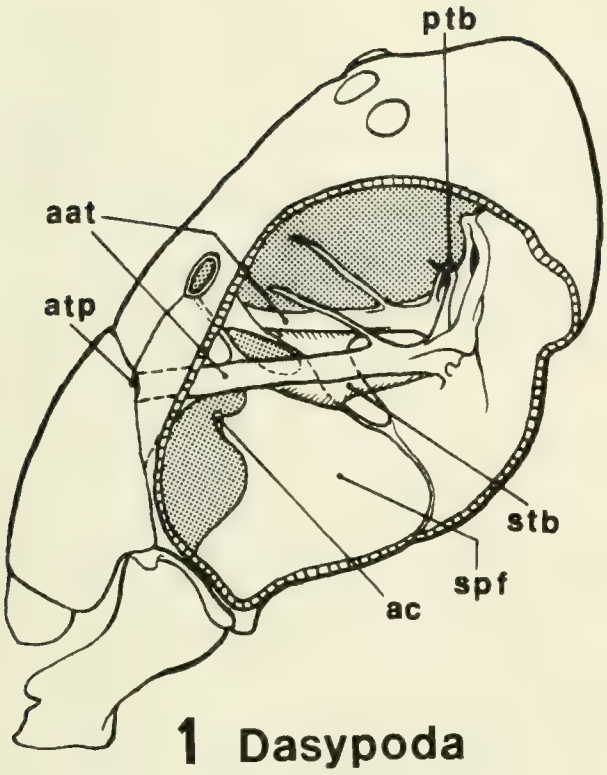
21. [NA] Epistomal suture below or lateral to anterior tentorial pits: (0) Extending straight or gently curved or angulate so that sides of clypeus diverge downward (Michener, 1944, figs. 1, 88-93). (1) Extending laterally upward and then downward, so that upper margin of clypeus is lobed. (2) Extending horizontally (MMD figs. 109, 331). (3) Angulate laterally near tentorial pit (Eickwort, 1969, fig. 1). This character is variable within the outgroup. States (1) and (2) are associated with a short, low clypeus which is probably ancestral for Aculeata according to Brothers and Carpenter (1993).

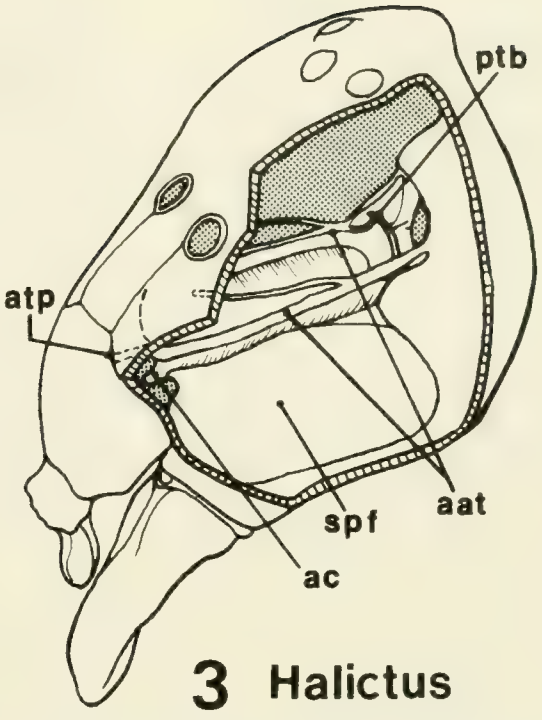
22. Attachment of cardo to articulatory process of head: (0) In middle third of head or behind (Michener, 1944, figs. 115, 116). (1) In anterior third but well behind clypeus (Michener, 1944, figs. 112, 113). (2) Just behind clypeus (Michener, 1944, fig. 114). State (0) characterizes the outgroup.

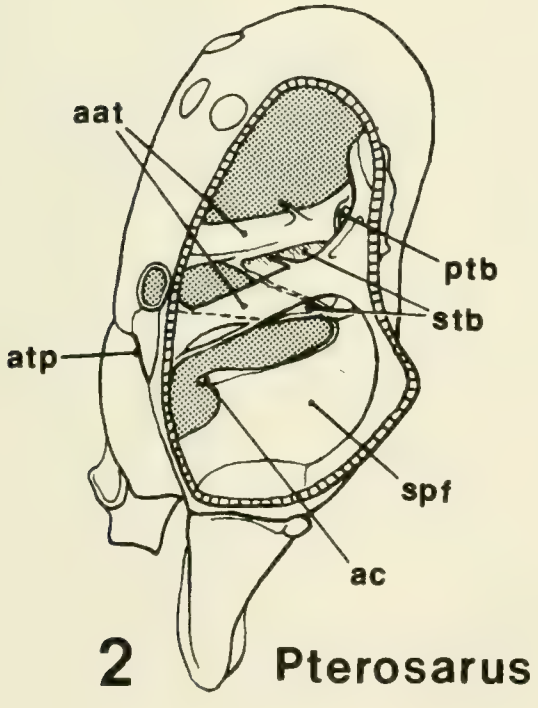
23. Cardo: (0) Broadened at apex, several times as wide as at base. (1) Slender, more or less parallel-sided (sometimes slightly enlarged apically, not over 2 times as wide as at base) (MMD figs. 7, 9). State (0) characterizes the outgroup.

24. Maxillary stipes with basal process (Winston, 1979, fig. 2b): (0) Not produced mesally. (1) Produced mesally, elongate. State (0) characterizes the outgroup.

25. Comb and concavity containing comb on distal posterior margin of maxillary stipes: (0) Absent (Winston, 1979, fig. 17). (1) Present (Winston, 1979, fig. 2a, 4a, d, h, j). When a comb is present it is always in a concavity except in *Lithurge,* which lacks the concavity and has a rather weak comb, but is coded (1). State (0) characterizes the outgroup. In some Nomadinae there is a concavity from which the comb was probably lost. In *Crawfordapis, Ctenocolletes, Hyleoides, Meroglossa,* and *Protandrena,* there is a weak concavity but no comb; they are coded (0). In *Eremaphanta*







Figs. 1-3. Dorsolateral views of heads of females of three species listed in Table 1, cut on approximately parasagittal planes to show the tentorium and related structure; **aat** = anterior arm of tentorium; **ac** = articulation of cardo; **atp** = anterior tentorial pit; **ptb** = primary tentorial bridge; **spf** = side of probiscidial fossa; **stb** = secondary tentorial bridge.

(Melittidae), not one of our exemplars, there is a concavity and comb, as in L-T bees (Michener, 1981a).

26. Inner surface of distal part of galea: (0) With comb, as in most spheciform wasps. (1) Without comb, as in bees. (*Corynura* has a weak distal comb.) The comb, state (0), is considered an ancestral feature; it is presumably lost in the spheciform wasps that lack it, although this has not been confirmed by a cladistic analysis. *Anoplius* has a comb while *Tiphia* does not.

27. Comb on inner surface of basal part of galea, mostly basal to palpus: (0) Absent. (1) Present (Michener, 1981a, figs. 10-13). (2) Large, on concave sclerotic margin, base elevated [as in *Hylaeus, Euryglossa* (Fig. 4)]. This comb is principally a character of S-T bees (including Melittidae) although *Xeromelecta* has a comb and *Deltoptila, Rhathymus,* and *Thyreus,* all in the Apidae, have a row of hairs in this area. State (0) characterizes the outgroup.

28. Base of galea: (0) Not tapering to point, often overlapping less than half length of stipes (Michener, 1981a, figs. 10-13). (1) Tapering gradually to point (sometimes membranous) overlapping at least half length of stipes (Michener, 1944, fig. 136) (not so long in *Chilicola*), or if not ending in a point, then extending to base of stipes. State (1) is found principally in Halictidae. State (0) characterizes the outgroup.

29. Posterior margin of galea with shoulder or lobe beyond palpus: (0) Absent. (1) Present. State (1) is found only in Hylaeinae and *Ctenoplectra;* state (0) characterizes the outgroup.

30. Row of bristles on internal surface of galeal blade: (0) Absent. (1) Present (R-AM fig. 15b), although sometimes limited to apical third or fourth of blade. State (0) characterizes the outgroup. These bristles arise from the midrib of the galeal blade, regarded by Roig-Alsina and Michener (1993) as the anterior margin of the sclerotized inner surface. Anterior to the midrib, the galeal blade lacks a lumen, the two surfaces being appressed together and commonly hairless, velumlike.

31. Distal part of galea: (0) A thick lobe. (1) A thin blade. All bees have state (1); the character is variable within the outgroup.

32. Galeal blade: (0) As wide as or wider than long, truncate, angulate, or broadly rounded. (1) Longer than wide, apex narrowly rounded or pointed. This character is variable among spheciform wasps, but preliminary analyses (Alexander, 1992a) indicate that state (0) is the groundplan state; in *Anoplius* the blade is short and broad but in *Tiphia* it is somewhat longer than broad, no doubt elongated independently from that of most bees.

33. [NA] Velum of galea (i.e., anterior, usually hairless area with inner and outer surfaces appressed, so that there is no lumen): (0) Tapering toward apex of galea (R-AM fig. 15b), sometimes leaving notch at distal end of velum. (1) Not much tapering, ending in strong notch or projection (Fig. 4). (2) Not well defined. The velum is the thin, nearly hairless, transparent area apparently with no lumen along the anterior edge of the galea. Most spheciform wasps have state (2), as do *Anoplius* and *Tiphia.*

34. Position of lacinia: (0) In normal position at base of galea (MMD figs. 411, 413). (1) Stretched up anterior surface of labiomaxillary tube so that the lacinia appears to be well up that tube (MMD fig. 412). State (0) characterizes the outgroup. State (1) is characteristic of the Halictidae.

35. [NA] Form of lacinia: (0) A rounded to elongate, often hairy, scalelike structure (MMD fig. 411). (1) A broad flap. (2) Finger-shaped (MMD fig. 412). (3) A hairy area, not well defined. (4) A strong blade, about half as long as galeal blade or more. (5) Not recognizable or merely hairless area. This character is variable within the outgroup. *Anoplius* has state (4); *Tiphia* lacks a recognizable lacinia.

36. Second and often first segment of maxillary palpus: (0) Without series of hairs along one side. (1) With longitudinal series of short setae along posterior side (Fig. 4). State (1) is found in Hylaeinae; state (0) is found in all others including the spheciform wasps.

37. Lorum: (0) Platelike or membranous, flat, or apex sometimes bent posteriorly as a flat, sclerotized projection (as in *Ctenocolletes*) (Michener, 1984, figs. 1, 3, 5). (1) Platelike but apex elevated and bent around base of mentum (Michener, 1984, fig. 31). (2) V-shaped with slender arms (MMD fig. 415; Michener, 1984, fig. 45). State (0) characterizes the outgroup. State (2) is found in Melittidae and L-T bees.

38. Apex of lorum and base of mentum: (0) Not projecting (MMD fig. 413). (1) Together projecting posteriorly as a short lobe from labiomaxillary tube (Michener, 1984, fig. 24). (2) As in (1) but lobe long (MMD fig. 414; Michener, 1984, fig. 18). State (0) characterizes the outgroup.

39. [NA] Mentum: (0) At least partly sclerotized, more or less rectangular (Michener, 1984, fig. 23). (1) Sclerotized, triangular, narrow and usually meeting lorum (Michener, 1984, figs. 43, 47). (2) Membranous or largely so (Michener, 1984, fig. 1). (3) Slightly sclerotized and completely fused to lorum (Michener, 1984, fig. 9) or absent. (4) A sclerotized

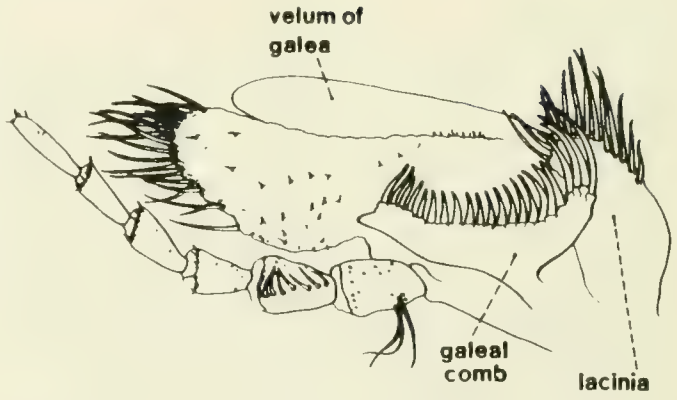


Fig. 4. Inner view of distal part of maxilla of *Hylaeus basalis* Smith.

longitudinal strip in membrane. This character is variable within the outgroup. State (0) is found in *Anoplius* and *Tiphia.*

40. Base of mentum: (0) Not curled to attach to lorum. (1) Curled to attach to or abut against lorum (Michener, 1984, fig. 46), as in melittids and L-T bees. State (0) characterizes the outgroup.

41. [NA] Origin of conjuctival thickening on prementum: (0) Near base of prementum. (1) One-fifth to one-third length of prementum from its base. (2) Over one-third to one-half length of prementum from its base. (3) Distal to middle of prementum. This character is variable within the outgroup. State (1) is found in *Anoplius* and *Tiphia.*

42. Base of prementum: (0) Without a fragmentum. (1) With a fragmentum isolated or partly isolated from rest of prementum (Michener, 1984, figs. 37, 43). State (0) characterizes the outgroup.

43. Prementum: (0) Length less than or equal to twice breadth. (1) Over twice as long as broad. This character is variable within the outgroup; *Anoplius* has state (0) and *Tiphia* has state (1).

44. Prementum: (0) Anterior surface wide open, i.e., membranous, and flat, so that a cross section would be about twice as wide as thick. (1) More or less tubular, cross section less than twice as wide as thick, sometimes almost circular. State (0) is the usual one in spheciform wasps, although *Philanthus* was coded as (1); *Tiphia* has state (1) and *Anoplius* has state (0).

45. Posterior surface of prementum: (0) Rather smooth, convex, sometimes with a median groove. (1) With large, flat area covered with short hairs or scales of uniform length. (2) With large, flat area or fovea margined by ridge or carina and covered with short hairs or scales of uniform length. State (0) characterizes the outgroup.

46. [NA] Anterior surface of prementum, near apex: (0) Unmodified. (1) With rounded, hairy, membranous projection. (2) With fingerlike membranous projection. (3) With flattened, fanlike projection. Most of the spheciform wasps and also *Anoplius* and *Tiphia* have state (0). *Sphecius,* which is coded (1), however, has a hairy projection quite different and presumably independently evolved from that of bees similarly coded.

47. Suspensorium of paraglossa: (0) With sparse hairs or row of bristles. (1) Densely hairy. This character is variable within the outgroup. *Anoplius* has state (1) and *Tiphia* has state (0).

48. Labial palpus segment 2: (0) Not particularly flattened, similar in form and usually in length to segments 3 and 4.

(1) Elongated compared to segments 3 and 4, usually flattened. State (1) is characteristic of L-T bees in general. State (0) characterizes the outgroup.

49. Labial palpus segment 1: (0) Not particularly flattened, similar in form to segments 3 and 4. (1) Elongate compared to segments 3 and 4, flattened in *Protoxaea, Systropha* and L-T bees. State (0) characterizes the outgroup. Usually this character varies with character 48, the first two segments being long and flattened in L-T bees and not in S-T bees. However, in various Oxaeinae, Panurginae and Rophitinae the first segment is much elongated and the second is not; for this reason the two are treated as separate characters.

50. Labial palpus, base of segment 1: (0) Parallel-sided or sides convergent basally. (1) Inner margin incised so that base is strongly narrowed (R-AM fig. 16). State (0) characterizes the outgroup.

51. First two segments of labial palpus: (0) Without membranous margins. (1) With membranous posterior margins. State (0) characterizes the outgroup.

52. [NA] Basiglossal sclerite: (0) A transverse band (sometimes broken medially) across base of glossa (Michener and Brooks, 1984, fig. 1). (1) More elongate, often longer than broad (sometimes medially cleft), laterally with posterior basal process extending around side of base of glossa (Michener and Brooks, 1984, fig. 7). (2) Absent. This character is variable within the outgroup.

53. [NA] Glossal shape: (0) Truncate or bilobed. (1) Pointed apically. (2) Bifid and drawn out into apicolateral points as in *Caupolicana.* (3) Long, linear (L-T bees). (4) Pointed apically in male, truncate or bilobed in female. (5) Rounded apically. State (0) characterizes the outgroup.

54. [NA] Annular hairs of glossa: (0) Acutely pointed, simple to lanceolate (Michener and Brooks, 1984, fig. 59e, g). (1) Branched or bifid at tips (Michener and Brooks, 1984, fig. 32b). (2) Short, blunt or capitate (Michener and Brooks, 1984, fig. 11c). (3) Short, blunt in female, longer in male. Spheciform wasps have very short, robust hairs, but their form is as in state (0), so this is the state that was assigned to all outgroup taxa in our analyses. However, the short, robust hairs of state (2) also resemble those of the outgroup and of *Anoplius* and *Tiphia,* so that this would be another defensible coding for the outgroup.

55. [NA] Preapical fringe of glossa: (0) Absent. (1) Present (Michener, 1992, fig. 1). (2) Present in female, absent or weak in male. State (0) characterizes the outgroup. The preapical fringe was illustrated and defined by McGinley (1980) and Michener (1992).

56. Annuli of glossa of female: (0) All relatively similar. (1) Divided into two sharply differentiated zones (Michener, 1992, fig. 1), or basal zone essentially without annuli. State (0) characterizes the outgroup. In *Anoplius* and *Tiphia* the hairs are not arranged in conspicuous rows or annuli.

57. [NA] Disannulate surface of glossa: (0) Exposed, nearly as large as annulate surface (Michener and Brooks, 1984, fig. 2). (1) Much narrower than annulate surface but not deeply invaginated (Michener and Brooks, 1984, figs. 5, 6). (2) Invaginated; annulate surface almost surrounding whole glossa (Michener and Brooks, 1984, fig. 8). (3) Exposed in female as in state (0), much narrower in male as in state (1) *(Meroglossa).* The outgroup has state (0). The rather flat (when not folded) glossa of spheciform wasps with a broadly exposed disannulate surface may be a derived feature of that group, for *Anoplius* and *Tiphia* have state (1).

58. [NA] Serriate hairs of glossa: (0) Not differentiated. (1) Converging, small (Michener and Brooks, 1984, fig. 10). (2) Diverging, large (Michener and Brooks, 1984, fig. 5), or small in *Systropha* (Michener and Brooks, 1984, fig. 36). (3) Not differentiated in female, large and diverging in male (Michener and Brooks, 1984, fig. 16). (4) Absent. State (0) characterizes the outgroup. Large hairs in other taxa such as *Anoplius* may or may not be homologues of serriate hairs of bees.

59. Glossal rod: (0) Absent. (1) Present (Michener and Brooks, 1984, figs. 9, 10). State (0) characterizes the outgroup and most S-T bees.

60. Flabellum: (0) Absent (Michener and Brooks, 1984, fig. 52F). (1) A flabellum-like structure present but not constricted at its base (Michener and Brooks, 1984, figs. 38A, 45). (2) Present, constricted at its base (Michener and Brooks, 1984, figs. 8, 101). A flabellum is absent in most S-T bees including most mellitids, but is present in Panurginae as well as L-T bees. No wasps have a flabellum, nor do any bees in which the glossa is blunt or rounded. There are all degrees of flabellar development, of which we recognize two levels, states (1) and (2).

61. [NA] Apical glossal zone or lobes derived from disannulate surface and with long, usually branched hairs (the glossal brush): (0) Absent. (1) Present (Michener, 1992, fig. 1). (2) Present in female, absent in male.

62. Apophyseal arms of prosternum: (0) Fused along median crest. (1) Separate from one another (Michener, 1944, figs. 26, 27). This character is variable within the outgroup.

63. [NA] Pre-episternal internal ridge (corresponding to external pre-episternal groove): (0) Directed ventrally or anteroventrally, more or less straight, reaching down far below level of pleural scrobe (MMD fig. 13; Michener, 1944, figs. 150, 152). (1) Curved posteriorly toward scrobe; in this case the corresponding external groove demarks the anterior and lower margins of the swollen hypoepimeral area (Michener, 1944, figs. 22, 149). (2) Short or absent, not reaching level of scrobe (Michener, 1944, fig. 153). (3) As in (0) but extending not or little below level of scrobe. (4) Internally as in (3) but externally depression as in (1). A long, straight ridge is present in most spheciform wasps and most S-T bees. A homologous internal ridge and external groove is not apparent in *Anoplius, Tiphia, Vespula,* etc.

64. Internal scrobal ridge from mesepisternal scrobe posteriorly to intersegmental suture: (0) Absent (Michener, 1944, fig. 149). (1) Present (Michener, 1944, figs. 148, 153). In most cases the state of this character was determined from the outside, in partly cleared material in which the internal ridge and external groove both were recognized as a darkening of the area. This character is variable within the outgroup.

65. [NA] Profile of metanotum: (0) Subhorizontal (MMD fig. 335). (1) Vertical (MMD figs. 379, 381). (2) Slanting (MMD fig. 215). State (0) characterizes the outgroup.

66. [NA] Propodeal profile: (0) With a nearly horizontal basal zone, twice as long as metanotum or less, behind which it rather abruptly turns downward to form the declivous posterior surface (MMD fig. 335). (1) With a steeply slanting or sometimes convex basal zone or entirely declivous (MMD figs. 166, 215). (2) With nearly horizontal basal zone three to eight times as long as metanotum. All bees in this study have either state (0) or state (1). State (2) is common in spheciform wasps but not in other aculeates such as *Anoplius* and *Tiphia.* State (0) occurs in two spheciform wasps included in this study.

67. Metapostnotum (propodeal triangle) with hairs: (0) Absent. (1) Present and widespread. This character is variable within the outgroup.

68. [NA] Membrane or sclerotization closing space behind metasternum and hind coxae and extending to base of S1: (0) Membrane arising beneath free apex of metasternum on ridge between the hind coxal condyles (R-AM fig. 24b). (1) Membrane arising from apical margin of metasternum, which therefore is not free (R-AM fig. 24c). (2) As in (1) but partly or almost entirely sclerotized. This character is variable within the outgroup.

69. Mid coxal shape: (0) Same as hind coxa, projecting from thorax, and only slightly smaller than hind coxa (Michener, 1981b, fig. 1). (1) Partly retracted into thorax, basicoxite enlarged and disticoxite reduced so that shape is very different from that of hind coxa (Michener, 1981b, fig. 15). Among the spheciform wasps, only *Tachytes* has state (1), as do bees; other Hymenoptera such as *Anoplius* and *Tiphia* as well as most spheciform wasps have state (0).

70. Dorsoventral length of mid coxa, measured between the two articulation points (see Michener, 1981b): (0) Much less than distance from summit of coxa to hind wing base. (1) About equal to that distance. State (0) characterizes the outgroup. Although state (0) was recorded for *Megandrena* and *Alocandrena* (and also occurs in some species of *Andrena*), it is quite unlike the state (0) of spheciform wasps.

71. Upper part and upper articulation of mid coxa: (0) Exposed (Michener, 1981b, fig. 12). (1) Hidden (Michener, 1981b, fig. 11). State (0) characterizes the outgroup.

72. [NA] Scopa on hind leg of female for carrying pollen: (0) Absent. (1) Principally on tibia and more or less on basitarsus (MMD fig. 116). (2) Developed on trochanter, femur, tibia and more or less on basitarsus (MMD fig. 117). Spheciform wasps do not provision nests with pollen and lack scopae; state (0) characterizes the outgroup. The same state also occurs in parasitic bees, which do not provision nests, and in Hylaeinae and Euryglossinae, which do.

73. [NA] Basitibial plate in female: (0) Absent. (1) Present (MMD fig. 283). (2) Weakly or incompletely defined (MMD fig. 174). State (0) characterizes the outgroup. Among bees, however, the plate often appears to be lost, as in parasitic apids, *Colletes*, etc.

74. Under surface of middle tibia of female: (0) Flat or convex with scattered hairs or hairless. (1) With obliquely longitudinal brush of hairs usually on a longitudinal ridge (mid tibial comb of Jander, 1976). State (0) characterizes the outgroup.

75. [NA] Inner margin of inner hind tibial spur of female: (0) Finely serrate to ciliate (as in MMD fig. 108). (1) Pectinate, with long, strong teeth (MMD figs. 161, 162). (2) Coarsely serrate (MMD fig. 153). State (0) characterizes the outgroup.

76. Outer hind tibial spur of female: (0) Finely serrate or ciliate (as in MMD fig. 108). (1) Coarsely serrate (as in MMD fig. 107). State (0) characterizes the outgroup.

77. Number of middle tibial spurs: (0) Two. (1) One. The spheciform wasps are variable, but all bees have state (1). This character has been considered phylogenetically informative in spheciform wasps (Bohart and Menke, 1976; Alexander, 1992a); it is used here to help resolve relationships within the outgroup.

78. [NA] Middle tibial spur: (0) Finely serrate or ciliate (MMD fig. 108). (1) Coarsely serrate (MMD fig. 107). (2) Pectinate. State (0) characterizes the outgroup.

79. Hind basitarsus of female: (0) Giving rise to second tarsomere at apex. (1) Projecting distad above articulation of second tarsomere as process without an apical brush (MMD fig. 117), or rarely *(Crawfordapis)* truncate with second tarsomere arising at lower edge, but with no actual projection above it. (2) Projecting distad as in (1) and ending in a small, dense brush (penicillus) (Eickwort, 1969, fig. 44). State (0) characterizes the outgroup.

80. Hind basitarsus: (0) As wide as following segments. (1) Wider than following segments. Spheciform wasps all have the ancestral state (0) and bees state (1). However, for some bees (Hylaeinae, Euryglossinae) the hind basitarsus is only slightly wider than the following segments and the difference is best recognized by comparing width of the first with the fourth or fifth tarsomeres.

81. Hind basitarsus: (0) With setose, often very weak, concavity forming with tibial spurs a strigil for cleaning the contralateral hind leg. (1) Without such a concavity and strigil. State (0) characterizes the outgroup. Bees all have state (1).

82. Claws of female: (0) Each with tooth, often large so that claw appears cleft, sometimes (in wasps) with two or more teeth. (1) Simple. This character varies within the outgroup.

83. Arolia: (0) Present. (1) Absent. State (0) characterizes the outgroup.

84. Number of submarginal cells in forewing: (0) Three. (1) Two. Both states occur within the outgroup as well as in bees, but parsimony analyses (e.g., Brothers and Carpenter, 1993; Alexander, 1992a) consistently show that state (0) is the groundplan condition for both spheciform wasps and bees. Reduction to two cells has occurred independently and perhaps even by different means. In most cases it is by loss of the second transverse cubital but in some, the first transverse cubital may be lost instead.

85. Distal part of wing: (0) Not papillate or weakly so (MMD fig. 229). (1) Strongly papillate (MMD fig. 228). State (0) characterizes the outgroup. State (1) is found among bees that are large and capable of rapid and often hovering flight.

86. Wing vestiture: (0) Hairy throughout. (1) Basal areas or all closed cells hairless. Most spheciform wasps and related Hymenoptera have state (0).

87. [NA] Stigma of forewing: (0) Longer than broad, length beyond vein r at least half as long as part basal to vein r, margin within marginal cell convex or sometimes straight (MMD fig. 57). (1) Longer than broad, length beyond vein r less than half as long as part basal to vein r, margin within marginal cell straight or concave (MMD fig. 53). (2) Small, about as long as broad to nearly absent (MMD fig. 63). This character is variable but limited to states (0) and (1) within the outgroup.

88. [NA] Jugal lobe of hind wing: (0) Long, half to eight-tenths length of vannal lobe (measured from wing base). (1) Short, over one-fourth to nearly one-half length of vannal lobe. (2) Shorter, one-fourth length of vannal lobe or less. (3) Absent. (4) Very long, nine-tenths as long as vannal lobe or more. This character is variable within the outgroup, and has been considered phylogenetically informative for spheciform wasps (e.g., Bohart and Menke, 1976; Alexander, 1992a) as well as for bees.

89. [NA] Vein cu-v of hind wing: (0) Shorter than second abscissa of vein M+Cu. (1) About as long as second abscissa of vein M+Cu (MMD fig. 233). (2) Over twice as long as second abscissa of vein M+Cu. (3) Meeting base of vein M so that there is no second abscissa of M+Cu. This character is variable within the outgroup.

90. Vein cu-v of hind wing: (0) Located basal to divergence of M. (1) Distal to divergence of M or approximately at that point. This character was included to help resolve outgroup relationships. All bees have state (0).

91. Female metasoma: (0) Sessile. (1) Petiolate, with petiole formed by S1 only. This character was included to help resolve outgroup relationships; state (1) is characteristic of all Sphecinae (with further modifications in some Ammophilini) and most Pemphredoninae (Bohart and Menke, 1976). All bees have state (0).

92. [NA] Gradulus of T2: (0) Directed backward at side, above and behind spiracle. (1) Directed toward or reaching spiracle. (2) Directed in front of spiracle. (3) Absent. This character is variable within the outgroup.

93. Metasomal sternal scopa of female: (0) Absent. (1) Hairs present, possibly a scopa. (2) Present. State (2) is principally a character of Megachilidae but certain Colletidae and Halictidae (*Homalictus*, not one of our ex-

emplars) have a strong metasomal scopa. Certain oil-collecting bees *(Ctenoplectra)* were also coded (2) although the sternal hairs function in gathering oil rather than carrying pollen and probably evolved independently from those of megachilids. Spheciform wasps, which do not collect pollen, have state (0).

94. T5 of female: (0) Without prepygidial fimbria, i.e., similar to preceding terga. (1) With prepygidial fimbria, hairs denser and longer than in hair bands of preceding terga. State (0) characterizes the outgroup.

95. Apex of T5 of female: (0) With polished margin of tergum absent or narrow and parallel-sided. (1) With broad, bare margin wider in middle than laterally and margined basally by long hairs. State (0) characterizes the outgroup and most bees.

96. T5 of female: (0) Without pseudopygidial area. (1) With pseudopygidial area (MMD figs. 220, 221). Spheciform wasps and most bees have state (0), which is ancestral. The pseudopygidial area is a feature of most female Nomadinae (Apidae).

97. [NA] T5 of female: (0) Without area of fine punctures and hairs middorsally, dividing prepygidial fimbria. (1) With such an area (MMD fig. 131). (2) With such an area, itself divided by deep cleft (MMD fig. 130). Wasps and most bees have state (0), which is plesiomorphic. States (1) and (2) are restricted to Halictidae.

98. [NA] T6 of female with pygidial plate: (0) Present. (1) Evident as apical margined process. (2) Absent. (3) Occupying whole dorsum of central and posterior part of tergum (homology not certain). (4) Represented by flat-topped spine (homology not certain). This character is variable within the outgroup. *Anoplius* and *Tiphia* have state (2).

99. Surface of T6 (or expanded pygidial plate) of female: (0) Not papillate, hairy except sometimes for pygidial plate. (1) Minutely papillate or roughened, hairless. State (1) is found only in the Fideliinae. The papillate area is perhaps the enlarged pygidial plate; see the discussion under character 98.

100. T7 of female: (0) With lateral areas connected by bridge. (1) Divided into two hemitergites. State (0) is characteristic of the outgroup. State (1) is characteristic of all bees.

101. [NA] Pygidial plate of T7 of male: (0) Present, distinct. (1) Absent, but sclerotized and often produced apical rim suggests apex of plate. (2) Absent, without apical rim. This character is variable within the outgroup. *Anoplius* and *Tiphia* have state (2).

102. [NA] S7 of male: (0) An ordinary-looking sternum although smaller than S6. (1) Rather like ordinary sternum but largely internal, without apical lobes. (2) Short, transverse, internal, without lobes. (3) Internal, disc of whole sternum membranous. (4) Internal, with two or four apical lobes or processes constricted at bases and arising close together on reduced disc of sternum. (5) Like (4) but bases of lobes broadly joined to disc of sternum which is frequently less reduced. (6) Internal, with median apical process and no lobes. State (0) characterizes the outgroup taxa used in this study, although nine tribes of spheciform wasps have male S7 reduced and partly or completely hidden by S6 (Alexander, 1992a, character 89).

103. [NA] S8 of male: (0) With single apical projection and usually moderate basolateral arms. (1) Without apical projection. (2) Bilobed apically. States (0) and (1) are both found among the spheciform wasps, but state (1) occurs only in the Sphecinae (*Sphex* and *Sceliphron* in this study).

104. Gonobase: (0) Forming a ring. (1) Almost absent. State (0) is found in all the spheciform wasps and most bees.

105. Ventral parapenial lobe of gonocoxite (R-AM fig. 33) or inferior gonostylar lobe: (0) Absent. (1) Present. This lobe may be the ventroapical plate of Allodapini (Michener, 1975). It may also be the retrorse lobe common in Halictinae and the ventral gonostylus of bees that appear to have double gonostyli. These homologies are uncertain, however, and the structures are here considered independent (see character 107). State (0) characterizes the outgroup.

106. Gonostylus: (0) Articulated to gonocoxite, although with partial fusion, or clearly differentiated by shape or constriction. (1) More or less indistinguishably fused to gonocoxite (or absent?), the resulting structure being called gonoforceps. All spheciform wasps included in our study except *Aphilanthops* and *Tachytes* have state (1). *Anoplius* and *Tiphia* have state (0).

107. [NA] Gonostylus: (0) Single. (1) Double, two nearly independent gonostylar structures arising from gonocoxite. (2) Absent. The ventral gonostylus is sometimes flexed basad (retrorse) as in many Halictinae. The code (1) is used in such cases as well as when the ventral gonostylus is directed downward or apicad. State (0) characterizes the outgroup.

108. [NA] Volsella: (0) Distinct, chelate. (1) A free sclerite but not chelate. (2) Absent or fused to gonocoxite. (3) Rudimentarily chelate, as in many halictids, andrenids, etc. In our outgroup, *Tachytes* and *Philanthus* have state (1), but the other spheciform wasps have state (0), as do *Anoplius* and *Tiphia*. Preliminary cladistic analyses of spheciform wasps (Alexander, 1992a) suggest that the form of volsella in *Tachytes* is a synapomorphy within the Larrinae, and the peculiar form of volsella in *Philanthus* is found only within the tribe Philanthini (Alexander, 1992b).

109. Dorsal bridge of penis valves: (0) Short, not extended behind level of apodemes, or absent. (1) Expanded posteriorly as spatha. The spatha is found only in certain bees; it is absent in all wasps. Fusion of the penis valves for a considerable distance, such as occurs in some spheciform wasps and in *Anoplius* and *Tiphia,* is entirely different from expansion of a bridge between the penis valves. Extended fusion is included in state (0) while the expanded bridge is state (1).

CHARACTERS FOR SERIES II ANALYSES

The characters used in Series II were the same as those used in Series I, and the states were coded in the same way, except as shown below. These revised codings, which employ nonredundant linear coding as presented by O'Grady and Deets (1987), were used to evaluate the phylogenetic implications of published hypotheses about the evolution of the glossa in bees, as explained in more detail in the following section. Characters that were recoded for the Series II analyses, but retained the same character number as in the Series I analyses, are italicized in the following discussion. Characters that received new numbers in the Series II analyses are not italicized.

53. Glossa shape, was partitioned into three characters. One of these, which retains the number 53 in the data matrix for Series II (Table 2), was treated as an additive character with the following five states: (0) Truncate or bilobed, as in spheciform wasps. (1) Pointed apically in both sexes. (2) Apex pointed in male, truncate or bilobed in female. (3) Truncate or bilobed in both sexes (this coding was used for colletid bees but not for spheciform wasps, despite the similarity of the shape of the glossa in both groups, for reasons that are explained in the following section). (4) Bifid and drawn out into apicolateral points as in *Caupolicana.*

The other two characters used for glossal shape are numbered 110 and 111 in the Series II data matrix (Table 2). In each case, the character was treated as having two states, with state (0) used for the majority of taxa and state (1)

used for a structure unique to one taxon or a small group of taxa in the analysis.

110. Glossal shape (second variable). (0) Not long and linear (coding used for all taxa except L-T bees). (1) Long and linear (coding used for L-T bees). Because it has been hypothesized that the long, linear glossa of L-T bees was derived from an ancestor in which the glossa was shorter but pointed apically, L-T bees received a coding of (1) for character 53 and (1) for character 110. They were coded (0) for character 111.

111. Glossal shape, third variable. (0) Not rounded apically (coding used for all taxa except *Ctenocolletes*.) (1) Rounded apically, as in *Ctenocolletes*. Because we did not wish to specify *a priori* which type of glossa was present in the common ancestor of *Ctenocolletes* and its (undetermined) sister taxon, *Ctenocolletes* was assigned a code of (?) for character 53 and (1) for character 111. It was coded (0) for character 110.

57. Disannulate surface of glossa, was partitioned into two characters. One of these, which retains the number 57 in the Series II data matrix (Table 2), was treated as an additive character with the following four states: (0) Exposed, rather flat (when not folded), about as broad as annulate surface (spheciform wasps). (1) Much narrower than annulate surface (Michener and Brooks, 1984, figs. 5, 6, 8). (2) Male as in state (1), female as in state (3). (3) Exposed and nearly as large as annulate surface in both sexes (Michener and Brooks, 1984, fig. 2). State (3) was used for Colletidae and Stenotritidae, in which the disannulate surface is nearly as broad and flat as in spheciform wasps.

112. Disannulate surface of glossa (second variable). (0) Not invaginated (used for all taxa except L-T bees). (1) Invaginated; annulate surface almost surrounding whole glossa (Michener and Brooks, 1984, fig. 8). L-T bees were coded as having state (1) for characters 57 and 112.

58. Serriate hairs of glossa, was partitioned into three characters. One of these, which retains the number 58 in the Series II data matrix (Table 2), was treated as an additive character with the following four states: (0) Not differentiated (this coding was used for spheciform wasps). (1) Diverging and large in both sexes. (2) Diverging and large in male, not differentiated in female. (3) Not differentiated in either sex (this coding was used for colletids and *Ctenocolletes*).

113. Serriate hairs of glossa (second variable). (0) Not converging and small (coding used for all taxa except *Ctenoplectra* and L-T bees). (1) Converging, small. *Ctenoplectra* and L-T bees received a coding of (1) for characters 58 and 113.

114. Serriate hairs of glossa (third variable). (0) Present. (1) Absent. *Hypomacrotera,* which has no hairs on the glossa, was coded (0) for characters 58 and 113, and (1) for character 114. With this coding, state 1 is an autapomorphy for *Hypomacrotera,* and adds no resolution to the phylogenetic analyses.

THE TWO SERIES OF ANALYSES

Two major theories as to the origin of the broad, truncate to bifid glossa of the Colletidae have been put forward. The *classical view,* reflected in the Series I analyses, has been that this glossal shape (states 53-0, 53-2) in colletids was derived from the similar glossal shape of spheciform wasps and other Hymenoptera and is therefore plesiomorphic among bees. Accompanying this character and presumably to be explained similarly are the broad disannulate surface of the glossa (state 57-0) and the lack of differentiated serriate hairs (state 58-0).

An alternative hypotheses for the evolution of these characters was suggested by Perkins (1912) and McGinley (1980), and supported by subsequent authors such as Michener and Brooks (1984) and Radchenko and Pesenko (1994). We refer to this as the *Perkins-McGinley view,* which is reflected in the Series II analyses. Some male colletids (e.g., *Meroglossa*) have a pointed glossa and the various features that go with this shape, such as the narrowed disannulate surface and well-developed serriate hairs. Furthermore, the broad glossa of female colletids is used to apply the glandular secretions that form the linings of their nest cells, and this function is not shared with spheciform wasps. Consequently, proponents of the Perkins-McGinley view hypothesize that the ancestral bee had a pointed glossa, which is still retained in a few male colletids as well as in noncolletid bees. The broad glossa and associated features are hypothesized to be apomorphies of the colletid lineage, as are the glossal brush (state 61-1) and preapical fringe (state 55-1, absent in Euryglossinae). These colletid features are thought to have originated and to function in females; to varying degrees they have been incorporated into male glossal structure except in *Meroglossa* and similar genera (Michener, 1992).

Thus, for characters 53, 57, and 58, the classical view, used in Series I, is that state (0) is homologous in spheciform wasps and colletids, and thus plesiomorphic for bees. The Perkins-McGinley view is that the structure coded as "state (0)" in the Series I analyses is independently derived in colletids and spheciform wasps; the character codings in Series II reflect this alternative interpretation of the evolution of these glossal characters.

METHODS OF ANALYSIS

Computer Programs. We used three computer programs, Hennig86 Version 1.5 (Farris, 1988), PAUP Version 3.1.1 (Swofford, 1993), and NONA Version 1.1 (Goloboff, 1993a), to search for minimum length trees. Because the size of our data matrices made exhaustive searches impractical, we employed approximate (= heuristic) searching procedures. In Hennig86, the command sequence "m*, bb*" was used. In PAUP, we experimented with several options and settled upon stepwise addition, addition sequence simple, 25 trees held at each step during stepwise addition, with TBR branch swapping and the MULPARS option in effect. In NONA, we used the following command sequence (because this is a new program and descriptions of the commands are currently available only from the

help file in the NONA program, a brief explanation of each command is provided below, and the name of each command is italicized and placed in parentheses and not abbreviated): *"hold*"* (to maximize the available memory for storing trees); *"empezar"* (to create a weighted Wagner tree and then rearrange it using subtree pruning-regrafting); *"hold/20"* (to hold a maximum of 20 trees in each replication of the *"mult"* command); *"mult*15"* (to perform 15 replicates of tree bisection-reconnection branch-swapping on an initial Wagner tree, with the sequence of taxa added randomly in each replicate). Because the program recommended swapping of trees found by the "mult*15" command, this sequence of commands was followed by *"max*"* (to implement more exhaustive branch swapping using tree bisection-reconnection). In the Series I analyses, NONA was the only program that succeeded in finding all minimum-length trees without overflowing the tree buffer memory. All analyses of family groundplans described below employed PAUP's branch-and-bound search option, which is an exact method (Swofford and Begle, 1993) for finding all minimum-length trees.

Character Weighting. Each of our analyses began by assigning equal weight to each character. We then examined the effects of weighting characters by means of two procedures, successive approximations (Farris, 1969) and implied weights (Goloboff, 1993b). The latter procedure was used in both series of analyses. In analyses employing the 65 exemplar taxa (as opposed to groundplan analyses), successive approximations could only be implemented in Series II. This is because memory limitations in PAUP and Hennig86, the programs that run successive approximations, render them unable to deal with the large number of trees that were found in Series I.

The successive approximations analyses (done with both PAUP and Hennig86) assigned weights as done by the "xsteps w" command of the Hennig86 program, which bases weights on the rescaled consistency index. This command calculates the maximum value of each character's rescaled consistency index, adjusted to a scale of 0 to 10, with scores truncated downward (e.g., a rescaled consistency index with any value greater than 4.0 and less than 5.0 would receive a weight of 4).

Goloboff's (1993b) implied weights procedure is implemented by his program Pee-Wee Version 2.1 (Goloboff, 1993c). The program's default weighting function, with k = 3, was used in our analyses. The commands used for tree searching were similar to those used with NONA: *"search =*" (similar to *empezar* command described above, but it also searches for additional trees, using tree bisection-reconnection; the = argument causes the order in which taxa are added when building the initial tree to be randomized); *"hold/20"; "mult*15"* (the last two commands are described in the first paragraph of the Methods of Analysis section). Tree searching with Pee-Wee is non-iterative, with the goal being to find the "fittest" tree(s). Goloboff (1993b) describes the "total fit" of a tree as follows: "The 'weight' of a character is a function of its fit to a tree, and so I will refer to the quantity to be maximized [by the implied weights procedure] as the 'total fit'. The fit for each character would be measured as a function of its homoplasy and the total fit of the tree would be the sum of the fits of its characters. Among all possible trees, the tree with the highest total fit would be chosen."

Character Polarization. As explained in several discussions of outgroups and character polarization (e.g., Farris, 1972; Meacham, 1984, 1986; Swofford and Begle, 1993; Nixon and Carpenter, 1993), the most efficient and logically sound way of polarizing characters with parsimony programs is to do a simultaneous parsimony analysis of the outgroup (in our study, 8 genera of spheciform wasps) and ingroup (48 genera of S-T bees and 9 of L-T bees). Sixty-seven of the characters in our analysis were invariant in the outgroup, so that polarization was simple and unequivocal. The other 42 characters varied in the outgroup. There is currently no well-supported hypothesis of phylogenetic relationships among spheciform wasps. A preliminary cladistic analysis by Alexander (1992a), based primarily upon adult morphological characters described by Bohart and Menke (1976) and larval characters described by Evans (summarized in Evans, 1959), found few unambiguous synapomorphies shared by the major lineages of spheciform wasps. Adult characters that might be synapomorphies at this level are included in our study, although many of them also vary among bees.

Various permutations of outgroup rooting were examined. They all produced the same tree topology for bees, and we have chosen to show our cladograms rooted with *Sphex* + *Sceliphron* as the monophyletic sister group of the rest of the genera in the analysis. When rooted in this way, the other six genera of spheciform wasps form a paraphyletic assemblage with respect to bees. This is consistent with one hypothesis of phylogenetic relationships among spheciform wasps, although we emphasize that those relationships are still poorly understood and that the present study was not undertaken to clarify them.

RESULTS

The following abbreviations will be used in presenting the results of our analyses: L = tree length (number of steps), ci = consistency index (Kluge and Farris, 1969), ri = retention index (Farris 1989a,b).

MONOPHYLY OF BEES

The monophyly of bees is strongly supported by this study.

This accords with traditional opinion and other cladistic analyses of aculeate Hymenoptera (e.g., Brothers, 1975; Lomholdt, 1982; Alexander, 1992a; Brothers and Carpenter, 1993). Autapomorphies for bees in our study are numerous and require no special discussion beyond what is stated in the List of Characters. Characters consistently found to be autapomorphies for bees in both Series I and Series II analyses are listed here for ready reference: **1-1** branched or plumose hairs; **6-1** anterior end of tentorium (subantennal suture connected to fan-shaped sheet of tentorium); **9-1** articulation of labrum with clypeus; **20-1** posterior end of proboscidial fossa (open except in *Protoxaea* and our two exemplars of Diphaglossini, *Cadeguala* and *Diphaglossa*); **23-1** shape of cardo; **33-0** velum of galea (two apomorphic states within bees); **47-0** suspensorium of paraglossa (with sparse hairs or row of bristles); **70-1** dorsoventral length of mid coxa (about equal to distance from summit of coxa to hind wing base); **74-1** mid tibial comb (absence in three of our exemplars, *Fidelia, Neofidelia,* and *Pararhophites,* interpreted as a single reversal); **80-1** hind basitarsus (wider than following segments); **81-1** hind basitarsus (without a concavity and strigil); **89-0** vein cu-v of hind wing (shorter than second abscissa of vein M+Cu except in *Caupolicana*); **100-1** T7 of female (divided into two hemitergites). A number of other apomorphic character states were consistently assigned to the groundplan for bees in our analyses, but were sufficiently variable among bees and/or the outgroup to make their polarity seem more equivocal than for the characters listed here.

SERIES I, PART 1: ANALYSES USING EXEMPLARS

Equal Weighting. This analysis employed 65 taxa and 109 characters; the data matrix is shown in Table 2. Of the three programs we used, only NONA is able to find and store a set of trees that does not exceed the program's memory capacity with our computers. NONA finds 4,296 trees with L = 711, ci = 0.27, ri = 0.69. The smaller sets of trees found by Hennig86 (2,438 trees) and PAUP (500 trees) have length and fit statistics identical to those found by NONA, and the strict consensus tree for each of these three sets of trees is the same (Fig. 5).

For the purposes of our study, the most noteworthy feature of this consensus tree is that there are major groups of genera that can be compared with traditionally recognized families of S-T bees. Halictidae as delimited by this analysis (all taxa subtended by node G on Fig. 5) corresponds exactly to that family as it is traditionally understood; node E subtends all genera of Colletidae in this study except exemplars of Euryglossinae (node B); and all genera of Andrenidae consistently cluster together, although this clade (node F) also contains *Protoxaea* (our sole exemplar of Oxaeidae) and *Ctenocolletes* (our sole exemplar of Stenotritidae). The genera of Melittidae form a basal polytomy within a monophyletic group (node H) that also includes *Ctenoplectra* (node N) and the L-T bees (node O); this group is called the MCL-T clade.

A few of the groupings on this consensus tree correspond to traditional S-T bee subfamilies, such as Diphaglossinae (node I) and Hylaeinae (node J) within the Colletidae, Panurginae (node K) within the Andrenidae; and Nomiinae (node L) within the Halictidae. However, at least as many traditional subfamilies, such as Colletinae, Andreninae, Halictinae, and Rophitinae, are not monophyletic groupings on this consensus tree. (All genera in the large clade at node M are in Halictinae, but *Nomioides* has also been considered to be in this subfamily.)

Relationships among the major families of S-T bees are poorly resolved. Euryglossines (node B) are the basal clade in this analysis, followed by the other colletids (node E). The remaining S-T bees are in a trichotomy (node D) involving three major clades: Andrenidae/Oxaeidae/Stenotritidae (node F), Halictidae (node G), and MCL-T clade (node H).

Successive Approximations Weighting. This procedure assigns a weight to each character according to its amount of homoplasy on a tree or a set of equally parsimonious trees; the higher the homoplasy, the poorer the "fit" of the character. In the latter case, when a given character might not show the same fit to each tree in a set, some criterion must be used for deciding which weight to use. Previous studies have generally given each character a weight corresponding to its maximum fit within the set of trees. We have followed this common convention, to facilitate comparison of our study with previous work, especially the study of L-T bees by Roig-Alsina and Michener (1993). (PAUP gives the user the option of using maximum, average, or minimum fit, whereas Hennig86 only calculates the maximum fit.)

The starting point for a successive approximations analysis is a set of trees that have been found to be most parsimonious when all characters are given equal weight. In the Series I data matrix, equal weighting yields 4,296 minimum length trees. With the computers available to us (a Zenith Z-386/33E and

Table 2. DATA MATRIX FOR THE ANALYSES IN SERIES I, PART 1, IN WHICH THE 65 GENERA LISTED IN TABLE 1 WERE USED AS TERMINAL TAXA. Characters that were coded differently for the analyses in Series II, Part 1 are also shown; these are characters 53a, 57a, 58a, and 110-114. →

Table 2, continued

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
1	Colletes	1	0	2	0	1	1	2	1	1	1	0	3	1	0	0	0	2	0	1	1	0	0	1	0	0	1	1
2	Caupolicana	1	1	1	0	0	1	1	1	1	0	0	3	1	0	0	0	2	0	0	1	0	0	1	0	0	1	1
3	Leioproctus	1	0	0	0	1	1	1	0	1	1	0	2	1	0	0	0	2	0	0	1	0	0	1	0	0	1	1
4	Callomelitta	1	0	0	0	0	1	4	1	1	0	0	2	1	0	0	1	2	0	1	1	0	1	1	1	0	1	1
5	Scrapter	1	0	0	0	1	1	2	0	1	0	0	3	1	0	0	0	2	0	1	1	0	2	1	0	0	1	1
6	Trichocolletes	1	0	1	0	1	1	0	1	1	1	0	2	1	0	0	0	2	0	1	1	0	1	1	0	0	1	1
7	Lonchopria	1	0	1	0	0	1	1	0	1	1	0	3	1	0	0	0	2	0	0	1	0	1	1	0	0	1	1
8	Eulonchopria	1	0	0	0	0	1	4	1	1	0	0	3	1	0	0	0	2	0	1	1	0	0	1	0	0	1	1
9	Cadeguala	1	1	0	0	1	1	0	1	1	0	0	2	1	0	0	0	2	0	0	0	0	1	1	0	0	1	1
10	Euryglossa	1	0	0	0	0	1	4	0	1	0	0	3	1	0	0	0	0	1	0	1	0	1	1	0	0	1	2
11	Hylaeus	1	0	0	0	1	1	4	0	1	0	0	2	1	0	0	0	2	0	0	1	0	0	1	0	0	1	2
12	Hyleoides	1	0	0	0	1	1	4	0	1	1	0	2	1	0	0	1	2	0	0	1	0	1	1	0	0	1	2
13	Amphylaeus	1	0	1	0	1	1	4	0	1	0	0	2	1	0	0	0	2	0	0	1	0	1	1	0	0	1	2
14	Chilicola	1	0	2	0	1	1	1	2	1	0	0	2	1	0	0	0	0	2	0	1	0	2	1	0	0	1	1
15	Euryglossula	1	0	1	0	0	1	4	0	1	0	0	3	1	0	0	0	0	1	0	1	0	0	1	0	0	1	1
16	Mourecotelles	1	0	2	0	0	1	1	0	1	0	0	2	1	0	0	0	2	0	1	1	0	0	1	0	0	1	1
17	Diphaglossa	1	0	1	0	1	1	1	2	1	0	0	0	1	0	0	1	2	0	1	0	0	1	1	0	0	1	1
18	Meroglossa	1	0	0	0	1	1	4	0	1	0	0	2	1	0	0	0	2	0	0	1	0	1	1	0	0	1	2
19	Crawfordapis	1	1	0	0	1	1	1	1	1	0	0	0	1	0	0	0	2	0	0	1	0	0	1	0	0	1	1
20	Mydrosoma	1	0	0	0	0	?	2	0	1	0	0	2	1	0	?	0	?	?	?	1	0	?	1	0	0	1	1
21	Ctenocolletes	1	1	1	1	0	1	1	0	1	0	0	3	1	0	0	0	2	0	0	1	0	1	1	0	0	1	1
22	Andrena	1	0	1	2	0	1	3	1	1	0	0	3	1	0	0	0	2	0	1	1	0	0	1	0	0	1	1
23	Protandrena	1	0	1	2	0	1	2	2	1	1	0	3	1	0	0	2	0	0	0	1	0	1	1	0	0	1	1
24	Hypomacrotera	1	0	1	2	0	1	2	2	1	2	0	3	1	0	0	2	1	0	0	1	0	1	1	0	0	1	1
25	Pterosarus	1	0	1	2	0	1	2	2	1	0	0	3	1	0	0	2	1	0	0	1	0	2	1	0	0	1	1
26	Eurherbilia	1	0	1	2	0	1	1	2	1	0	0	3	0	0	0	2	2	0	1	1	0	1	1	0	0	1	1
27	Megandrena	1	0	1	2	0	1	3	2	1	0	0	3	1	0	0	2	2	0	1	1	0	1	1	0	0	1	1
28	Alocandrena	1	0	1	2	0	1	5	2	1	0	0	2	0	0	0	0	2	0	1	1	0	1	1	0	0	1	1
29	Protoxaea	1	1	1	2	0	1	1	2	1	2	1	1	1	0	0	2	2	0	1	0	0	1	1	0	0	1	1
30	Dieunomia	1	0	2	0	0	1	0	0	1	0	0	3	1	1	0	0	2	0	2	1	0	2	1	0	0	1	1
31	Nomia	1	0	2	0	0	1	0	0	1	0	0	3	1	1	0	0	2	0	2	1	0	2	1	0	0	1	1
32	Dufourea	1	0	0	0	0	1	1	1	1	1	0	2	1	0	0	0	0	2	2	1	0	2	1	0	0	1	0
33	Systropha	1	0	0	0	0	1	1	1	1	0	0	2	1	0	0	0	0	2	2	1	2	2	1	0	0	1	0
34	Corynura	1	0	0	0	0	1	0	1	1	0	0	3	1	1	0	0	0	3	2	1	0	2	1	0	0	1	1
35	Pseudaugochlora	1	0	0	0	1	1	0	1	1	0	0	3	1	1	0	0	0	2	2	1	3	2	1	0	0	1	0
36	Augochlora	1	0	0	0	0	1	0	1	1	0	0	3	1	1	0	0	0	3	2	1	3	2	1	0	0	1	0
37	Halictus	1	0	0	0	0	1	1	1	1	0	0	3	1	1	0	0	0	3	2	1	0	2	1	0	0	1	0
38	Nomioides	1	0	1	0	1	1	0	1-	1	0	0	3	1	0	0	0	0	3	2	1	1	2	1	0	0	1	0
39	Agapostemon	1	0	2	0	1	1	0	1	1	0	0	3	1	1	0	0	0	3	2	1	3	2	1	0	0	1	0
40	Sphecodes	1	0	0	0	0	1	0	0	1	0	0	3	1	0	0	0	0	3	2	1	2	2	1	0	0	1	0
41	Conanthalictus	1	0	2	0	0	1	1	0	1	0	0	2	1	0	0	0	0	3	2	1	2	2	1	0	0	1	0
42	Meganomia	1	0	0	0	0	1	0	0	1	0	0	3	1	0	1	0	2	1	1	1	0	0	1	1	0	1	1
43	Macropis	1	0	0	0	0	1	0	0	1	0	0	3	1	0	1	0	2	0	1	1	0	0	1	0	0	1	1
44	Hesperapis	1	0	0	0	0	1	1	0	1	0	0	3	1	0	2	0	2	0	1	1	0	0	1	0	0	1	1
45	Dasypoda	1	0	0	0	0	1	1	1	1	0	0	3	1	0	2	0	2	0	1	1	0	0	1	0	0	1	0
46	Melitta	1	0	0	0	0	1	1	1	1	1	0	3	1	0	2	0	2	2	1	1	0	0	1	0	0	1	1
47	Xeralictus	1	0	0	0	0	1	0	1	1	1	0	2	1	0	0	0	0	3	2	1	0	2	1	0	0	1	1
48	Ctenoplectra	1	0	2	0	1	1	0	2	1	0	0	3	0	0	2	0	2	2	1	1	0	0	1	1	1	1	0
49	Neofidelia	1	0	0	0	0	1	1	1	1	2	2	1	1	0	0	0	1	2	0	1	0	0	1	1	1	1	0
50	Pararhophites	1	0	0	0	0	1	0	0	1	0	1	1	0	0	0	2	1	2	0	1	0	0	1	1	0	1	0
51	Lithurge	1	0	1	0	0	1	0	0	1	0	2	1	0	0	0	0	1	0	1	1	0	1	1	1	1	1	0
52	Exomalopsis	1	0	0	0	0	1	1	1	1	0	0	1	0	0	1	2	2	2	1	1	0	1	1	1	1	1	0
53	Manuelia	1	0	0	0	0	1	1	0	1	1	0	3	0	0	0	0	0	0	1	1	0	1	1	1	1	1	0
54	Nomada	1	0	0	0	1	1	0	2	1	2	0	1	0	0	0	2	1	2	1	1	0	1	1	1	0	1	0
55	Triepeolus	1	0	0	0	0	1	0	2	1	2	0	1	0	0	1	2	2	1	1	1	0	1	1	1	1	1	0
56	Haplomelitta	1	0	0	0	0	1	0	1	1	0	0	3	1	0	2	0	2	0	1	1	0	1	1	0	0	1	0
57	Fidelia	1	0	0	0	0	1	1	1	1	2	2	1	0	0	0	0	1	2	0	1	0	0	1	1	0	1	0
58	Aphilanthops	0	0	2	0	1	0	1	0	0	0	0	0	0	0	0	2	0	1	0	0	1	0	0	0	0	0	0
59	Philanthus	0	0	2	0	1	0	1	0	0	0	0	0	0	0	0	2	0	1	0	0	1	0	0	0	0	0	0
60	Passaloecus	0	0	?	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
61	Tachytes	0	0	3	0	0	0	0	0	0	0	0	2	1	0	0	2	0	0	0	0	1	0	0	0	0	0	0
62	Sphecius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
63	Sphex	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0
64	Astata	0	0	3	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	1	0
65	Sceliphron	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	0	0	0	0	0	0	0	0	0

Table 2, continued

		28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54
1	Colletes	0	0	0	1	1	0	0	0	0	1	0	0	0	2	0	1	1	0	1	0	0	0	0	0	0	0	2
2	Caupolicana	0	0	0	1	1	0	0	0	0	1	1	0	0	1	0	1	1	0	1	0	0	0	0	0	0	2	3
3	Leioproctus	0	0	0	1	1	0	0	0	0	1	1	2	0	2	0	1	1	0	0	0	0	0	0	0	0	0	3
4	Callomelitta	0	0	0	1	1	0	0	0	0	1	0	2	0	2	0	1	1	0	0	0	0	0	0	0	0	0	3
5	Scrapter	0	0	0	1	1	0	0	0	0	1	1	1	1	2	0	1	1	2	0	0	0	0	0	0	0	0	3
6	Trichocolletes	0	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	3
7	Lonchopria	0	0	0	1	1	0	0	0	0	2	1	1	1	2	0	1	1	0	0	0	0	0	0	0	0	0	3
8	Eulonchopria	0	0	0	1	1	0	0	0	0	1	1	0	1	2	0	1	1	0	0	0	0	0	0	0	0	0	3
9	Cadeguala	0	0	0	1	1	0	0	0	0	1	1	0	0	2	0	1	1	0	0	0	0	0	0	0	0	2	3
10	Euryglossa	0	0	0	1	0	1	0	1	0	1	0	2	0	2	0	1	0	1	1	0	0	0	0	0	0	0	3
11	Hylaeus	0	1	0	1	1	1	0	4	1	0	0	2	0	2	0	1	1	2	2	0	0	0	0	0	0	0	3
12	Hyleoides	0	1	0	1	1	1	0	4	1	0	0	2	0	2	0	1	1	2	2	0	0	0	0	0	0	0	3
13	Amphylaeus	0	1	0	1	1	1	0	4	1	0	0	2	0	2	0	1	1	2	2	0	0	0	0	0	0	4	3
14	Chilicola	1	0	0	1	1	1	0	5	0	0	0	2	0	2	0	1	1	2	0	0	0	0	0	0	0	0	3
15	Euryglossula	0	0	0	1	0	0	0	1	0	0	0	2	0	3	0	1	0	1	3	0	0	0	0	0	0	0	3
16	Mourecotelles	0	0	0	1	1	0	0	0	0	1	0	0	0	2	0	1	1	0	1	0	0	0	0	0	0	0	3
17	Diphaglossa	0	0	0	1	1	0	0	0	0	1	1	0	0	2	0	1	1	0	0	0	0	0	0	0	0	2	3
18	Meroglossa	0	1	0	1	1	1	0	4	1	0	0	2	0	2	0	1	1	2	2	0	0	0	0	0	0	4	3
19	Crawfordapis	0	0	0	1	1	0	0	0	0	1	1	0	0	1	0	1	1	0	1	0	0	0	0	0	0	2	3
20	Mydrosoma	0	0	0	1	1	0	0	0	0	1	0	0	0	2	0	1	1	0	1	0	0	0	0	0	0	2	3
21	Ctenocolletes	0	0	0	1	1	0	0	0	0	0	1	2	0	2	0	1	1	0	0	0	0	0	0	0	0	5	2
22	Andrena	0	0	0	1	1	0	0	0	0	1	1	2	0	2	1	1	1	0	0	0	0	0	0	0	0	1	0
23	Protandrena	0	0	0	1	1	0	0	0	0	1	1	2	0	1	1	1	1	0	0	0	0	1	0	0	0	1	0
24	Hypomacrotera	0	0	0	1	1	0	0	0	0	1	0	2	0	1	1	1	1	0	0	0	0	1	1	0	0	3	0
25	Pterosarus	0	0	0	1	1	0	0	0	0	1	1	2	0	0	1	1	1	0	0	0	0	1	0	0	0	3	0
26	Euherbstia	0	0	0	1	1	0	0	0	0	1	1	0	1	2	0	1	1	0	0	0	0	0	0	0	0	1	0
27	Megandrena	0	0	0	1	1	0	0	0	0	1	1	2	1	2	0	1	1	0	0	0	0	1	0	0	0	1	0
28	Alocandrena	0	0	0	1	1	0	0	0	0	1	1	2	1	2	1	1	1	0	0	0	0	0	0	0	0	1	0
29	Protoxaea	0	0	0	1	1	2	0	0	0	0	0	3	0	1	0	1	1	0	0	0	0	1	0	0	0	1	0
30	Dieunomia	1	0	0	1	1	0	1	2	0	1	0	3	0	1	0	1	1	0	0	0	0	0	0	0	0	1	1
31	Nomia	1	0	0	1	1	0	1	2	0	1	0	3	0	1	0	1	1	0	0	0	0	1	0	0	0	1	1
32	Dufourea	1	0	0	1	1	0	1	2	0	0	0	2	0	1	0	1	1	0	0	0	0	0	1	0	0	1	1
33	Systropha	1	0	0	1	1	0	1	2	0	1	0	2	0	1	0	1	1	0	0	0	0	1	1	0	0	0	1	1
34	Corynura	1	0	0	1	1	0	1	2	0	0	0	2	0	1	0	1	1	0	0	0	0	0	0	0	0	0	1	0
35	Pseudaugochlora	1	0	0	1	1	0	1	2	0	0	0	2	0	0	0	1	1	0	0	0	0	1	0	0	0	1	1
36	Augochlora	1	0	0	1	1	0	1	2	0	0	0	2	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1
37	Halictus	1	0	0	1	1	0	1	2	0	0	0	2	0	1	0	1	1	0	0	0	0	0	0	0	0	1	1
38	Nomioides	1	0	0	1	1	0	1	2	0	0	0	2	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0
39	Agapostemon	1	0	0	1	1	0	1	2	0	0	0	2	0	0	0	1	1	0	0	0	0	1	0	0	0	1	1
40	Sphecodes	1	0	0	1	1	0	1	2	0	0	0	2	0	1	0	1	1	0	0	0	0	0	0	0	0	1	1
41	Conanthalictus	1	0	0	1	1	0	1	2	0	0	1	2	0	1	0	1	1	0	0	0	0	0	0	0	0	1	0
42	Meganomia	0	0	0	1	1	0	0	0	0	2	2	1	1	1	1	1	1	0	0	0	0	0	0	0	0	1	0
43	Macropis	0	0	0	1	1	0	0	0	0	2	2	1	1	2	1	1	1	0	0	0	0	0	0	0	0	1	0
44	Hesperapis	0	0	0	1	1	0	0	0	0	2	2	1	1	0	1	1	1	0	0	0	0	0	0	0	0	1	0
45	Dasypoda	0	0	0	1	1	0	0	0	0	2	2	1	1	1	1	1	1	0	0	0	0	0	0	0	0	1	0
46	Melitta	0	0	0	1	1	0	0	0	0	2	2	1	1	0	1	1	1	0	0	0	0	0	0	0	0	1	0
47	Xeralictus	1	0	0	1	1	0	1	2	0	1	0	2	0	1	0	1	1	0	0	0	0	0	0	0	0	1	0
48	Ctenoplectra	0	1	0	1	1	0	0	0	0	2	2	1	1	0	1	1	1	0	0	0	0	0	0	0	1	1	0
49	Neofidelia	0	0	0	1	1	0	0	0	0	2	2	1	1	0	0	1	1	0	0	0	1	1	0	0	1	3	0
50	Pararhophites	0	0	1	1	1	0	0	0	0	2	2	1	1	0	0	1	1	0	0	0	1	1	0	1	1	3	0
51	Lithurge	0	0	1	1	1	0	0	0	0	2	2	1	0	0	0	1	1	0	0	0	1	1	1	1	1	3	0
52	Exomalopsis	0	0	1	1	1	0	0	0	0	2	2	1	1	0	0	1	1	0	0	0	1	1	1	0	1	3	0
53	Manuelia	0	0	1	1	1	0	0	0	0	2	2	1	1	0	0	1	1	0	0	0	1	1	1	1	1	3	0
54	Nomada	0	0	1	1	1	0	0	0	0	2	2	1	1	0	0	1	1	0	0	0	1	1	0	0	1	3	0
55	Triepeolus	0	0	0	1	1	0	0	0	0	2	2	1	1	0	0	1	1	0	0	0	1	1	0	1	1	3	0
56	Haplomelitta	0	0	0	1	1	0	0	0	0	2	2	1	1	0	1	1	1	0	0	0	0	0	0	0	0	1	0
57	Fidelia	0	0	0	1	1	0	0	0	0	2	2	1	1	0	0	1	1	0	0	0	1	1	0	1	1	3	0
58	Aphilanthops	0	0	0	0	0	2	0	4	0	0	0	4	0	3	0	0	0	0	0	0	0	0	0	0	0	1	0	0
59	Philanthus	0	0	0	0	0	2	0	4	0	0	0	4	0	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0
60	Passaloecus	0	0	0	0	0	2	0	3	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
61	Tachytes	0	0	0	1	1	2	0	0	0	0	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0
62	Sphecius	0	0	0	1	0	2	0	4	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
63	Sphex	0	0	0	1	1	0	0	0	0	0	0	0	0	2	0	1	0	0	0	1	0	0	0	0	2	0	0
64	Astata	0	0	0	0	0	2	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
65	Sceliphron	0	0	0	1	0	2	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0

Table 2, continued

		55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81
1	Colletes	.	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	2	0	1	0	0	1	0	0	1	1
2	Caupolicana	2	0	0	0	0	0	1	0	0	1	2	1	0	1	1	1	1	2	2	1	0	0	1	0	1	1	1
3	Leioproctus	2	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	2	1	1	1	0	1	0	0	1	1
4	Callomelitta	2	0	0	0	0	0	1	0	0	0	2	0	0	0	1	1	1	2	1	1	0	0	1	0	0	1	1
5	Scrapter	1	0	0	0	0	0	1	0	0	0	0	1	0	1	1	1	1	2	1	1	0	0	1	0	0	1	1
6	Trichocolletes	2	0	0	0	0	0	1	0	0	1	0	1	0	1	1	1	1	2	2	1	1	0	1	0	0	1	1
7	Lonchopria	2	0	0	0	0	0	1	0	0	0	2	1	0	1	1	1	1	2	1	1	1	0	1	0	0	1	1
8	Eulonchopria	2	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	2	1	1	1	0	1	0	0	1	1
9	Cadeguala	2	0	0	0	0	0	1	0	1	1	2	1	0	1	1	1	1	2	2	1	0	0	1	0	1	1	1
10	Eurygloss a	0	1	0	0	0	0	1	0	0	0	0	1	0	1	1	1	1	0	1	1	1	0	1	0	0	1	1
11	Hylaeus	2	1	0	0	0	0	1	0	0	1	0	1	0	1	1	1	1	0	0	1	0	0	1	0	0	1	1
12	Hyleoides	2	1	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	0	0	1	0	0	1	0	1	1	1
13	Amphylaeus	2	1	0	0	0	0	1	0	0	1	0	1	0	1	1	1	1	0	0	1	0	0	1	0	0	1	1
14	Chilicola	1	0	0	0	0	0	1	0	0	1	0	0	0	1	1	1	1	2	0	1	0	0	1	0	0	1	1
15	Euryglossula	0	1	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	0	1	1	0	0	1	0	0	1	1
16	Mourecotelles	2	0	0	0	0	0	1	0	0	0	2	1	0	1	1	1	1	2	0	1	0	0	1	0	0	1	1
17	Diphaglossa	2	0	0	0	0	0	1	0	1	1	2	1	0	1	1	1	1	2	2	1	0	0	1	0	1	1	1
18	Meroglossa	2	1	3	3	0	0	2	0	0	1	0	0	0	1	1	1	1	0	0	1	0	0	1	0	0	1	1
19	Crawfordapis	2	0	0	0	0	0	1	0	0	1	1	1	0	1	1	1	1	2	2	1	0	0	1	0	1	1	1
20	Mydrosoma	2	0	0	0	0	0	1	?	1	1	2	1	0	1	1	1	1	2	2	1	0	0	1	0	1	1	1
21	Ctenocolletes	0	0	0	0	0	0	0	?	1	1	2	1	0	1	1	1	1	2	1	1	1	0	1	2	1	1	1
22	Andrena	0	0	1	2	0	0	0	0	1	0	0	1	0	1	1	1	1	2	1	1	0	0	1	0	1	1	1
23	Protandrena	0	0	1	2	0	0	0	0	3	0	0	0	0	1	1	1	1	1	1	1	0	0	1	2	1	1	1
24	Hypomacrotera	0	0	1	4	0	2	0	0	3	0	0	0	0	1	1	1	1	1	1	1	0	0	1	0	1	1	1
25	Pterosarus	0	0	1	2	0	0	0	0	3	0	0	0	0	1	1	1	1	1	2	1	0	0	1	2	1	1	1
26	Eurherbia	0	0	1	2	0	0	0	0	1	1	0	1	0	1	1	1	1	2	1	1	1	0	1	0	1	1	1
27	Megandrena	0	0	1	2	0	0	0	0	1	1	0	0	0	1	1	0	1	2	1	1	0	0	1	0	1	1	1
28	Alocandrena	0	0	1	2	0	0	0	0	1	1	0	1	0	1	1	0	1	1	1	1	0	0	1	0	1	1	1
29	Protoxaea	0	0	1	2	0	0	0	0	3	1	2	1	0	1	1	1	1	2	1	1	0	0	1	0	1	1	1
30	Dieunomia	0	0	1	2	0	0	0	0	3	0	0	0	0	1	1	1	1	2	1	1	0	0	1	0	2	1	1
31	Nomia	0	0	1	2	0	0	0	0	3	0	2	1	0	1	1	1	1	2	1	1	0	0	1	0	2	1	1
32	Dufourea	0	0	1	2	0	1	0	0	0	0	0	0	0	1	1	1	1	2	1	1	0	0	1	0	1	1	1
33	Systropha	0	0	1	2	0	1	0	0	0	1	0	0	0	1	1	1	1	1	1	1	0	0	1	0	1	1	1
34	Corynura	0	0	1	2	0	0	0	0	0	0	0	0	0	1	1	1	1	2	2	1	1	0	1	0	2	1	1
35	Pseudaugochlora	0	0	2	2	0	0	0	0	0	0	0	0	0	1	1	1	1	2	1	1	1	0	1	0	2	1	1
36	Augochlora	0	0	1	2	0	0	0	0	0	0	0	0	0	1	1	1	1	2	1	1	0	0	1	0	2	1	1
37	Halictus	0	0	1	2	0	0	0	0	0	0	0	0	0	1	1	1	1	2	1	1	1	0	1	0	2	1	1
38	Nomioides	0	0	1	2	0	1	0	0	0	0	0	0	0	1	1	1	1	2	1	1	1	0	1	0	2	1	1
39	Agapostemon	0	0	1	2	0	0	0	0	0	0	0	0	0	1	1	1	1	2	1	1	1	0	1	0	2	1	1
40	Sphecodes	0	0	1	2	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	1	0	0	1	0	1	1	1
41	Conanthalictus	0	0	1	2	0	0	0	0	0	1	0	0	0	1	1	1	1	2	1	1	0	0	1	0	0	1	1
42	Meganomia	0	0	1	2	0	0	0	1	2	1	1	1	0	1	1	1	0	1	2	1	0	0	1	0	0	1	1
43	Macropis	0	0	1	2	0	0	0	1	2	0	2	1	0	1	1	1	0	1	1	1	0	0	1	0	1	1	1
44	Hesperapis	0	0	1	2	0	0	0	1	2	1	2	1	0	1	1	1	0	1	1	1	0	0	1	2	0	1	1
45	Dasypoda	0	0	1	2	0	1	0	1	2	1	2	1	0	1	1	1	0	1	0	1	0	0	1	0	0	1	1
46	Melitta	0	0	1	2	0	0	0	1	2	0	2	1	0	1	1	1	0	1	1	1	0	0	1	0	1	1	1
47	Xeralictus	0	0	1	2	0	0	0	0	1	1	0	0	0	1	1	1	1	1	1	1	2	0	1	1	1	1	1
48	Ctenoplectra	0	0	1	1	0	2	0	1	1	0	0	0	1	1	1	1	0	1	1	1	0	0	1	0	1	1	1
49	Neofidelia	0	0	2	1	1	2	0	0	4	0	2	1	0	1	1	1	0	1	2	0	2	1	1	1	0	1	1
50	Pararhophites	0	0	2	1	1	2	0	0	2	0	2	0	1	1	1	1	0	1	2	0	2	1	1	1	0	1	1
51	Lithurge	0	0	2	1	1	2	0	0	2	0	2	1	1	1	1	1	0	0	2	1	0	0	1	0	0	1	1
52	Exomalopsis	0	0	2	1	1	2	0	0	1	0	2	1	1	1	1	1	0	1	1	1	0	0	1	0	2	1	1
53	Manuelia	0	0	2	1	1	2	0	1	1	1	1	1	0	1	1	1	0	1	1	1	0	0	1	0	1	1	1
54	Nomada	0	0	2	1	1	1	0	0	1	0	1	1	0	0	1	1	0	0	0	1	0	0	1	0	0	1	1
55	Triepeolus	0	0	2	1	1	1	0	0	1	0	1	1	1	0	1	1	0	0	0	1	0	0	1	0	0	1	1
56	Haplomelitta	0	0	1	2	0	0	0	1	2	1	2	1	0	1	1	1	0	1	1	1	0	0	1	1	1	1	1
57	Fidelia	0	0	2	1	1	2	0	0	1	0	2	1	1	1	1	1	0	1	2	0	2	1	1	1	0	1	1
58	Aphilanthops	0	0	0	0	0	0	0	1	0	1	0	2	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0
59	Philanthus	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0
60	Passaloecus	0	0	0	0	0	0	0	1	0	0	0	2	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0
61	Tachytes	0	0	0	0	0	0	0	0	0	0	0	2	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0
62	Sphecius	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0
63	Sphex	0	0	0	0	0	0	0	0	0	0	0	2	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0
64	Astata	0	0	0	0	0	0	0	0	0	1	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
65	Sceliphron	0	0	0	0	0	0	0	0	0	0	0	2	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 2, continued

		82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108
1	Colletes	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	1	2	4	0	0	0	0	0	0
2	Caupolicana	0	0	0	1	0	1	0	1	0	0	0	1	1	0	0	0	0	0	1	2	4	0	0	0	1	0	0
3	Leioproctus	0	0	0	0	0	0	0	0	0	0	1	2	1	0	0	0	0	0	1	2	4	0	0	0	1	0	3
4	Callomelitta	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	2	4	0	0	0	1	0	3
5	Scrapter	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	2	4	0	0	1	0	0	1
6	Trichocolletes	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	2	4	0	0	0	1	0	3
7	Lonchopria	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	2	4	0	0	0	0	1	1
8	Eulonchopria	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	2	4	0	0	0	0	0	3
9	Cadeguala	0	0	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0	0	1	2	4	0	0	0	1	0	3
10	Euryglossa	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	2	4	0	0	0	0	0	0
11	Hylaeus	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	1	2	5	0	0	0	1	0	3
12	Hyleoides	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	2	0	1	2	4	0	0	0	1	0	3
13	Amphylaeus	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	1	2	4	0	0	0	1	0	3
14	Chilicola	0	0	1	0	0	0	0	0	0	0	0	2	0	0	0	0	2	0	1	2	4	0	0	0	1	0	3
15	Euryglossula	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	2	4	0	0	0	1	0	3
16	Mourecotelles	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	2	0	1	2	4	0	0	0	0	0	0
17	Diphaglossa	0	0	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0	0	1	2	4	0	0	0	1	0	3
18	Meroglossa	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0	1	2	4	0	0	0	1	0	3
19	Crawfordapis	0	0	0	1	0	2	4	0	0	0	1	1	1	0	0	0	0	0	1	2	5	0	0	0	0	0	0
20	Mydrosoma	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	?	2	4	0	0	0	0	0	3
21	Ctenocolletes	0	0	0	1	0	1	0	0	0	0	2	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1
22	Andrena	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	0	0	1	0	3
23	Protandrena	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	2	5	0	1	0	0	0	3
24	Hypomacrotera	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	5	0	1	0	?	2	1
25	Pterosarus	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	2	5	0	1	0	0	0	3
26	Euherbstia	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	1	2	0	0	0	0	1	0	1
27	Megandrena	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	1	5	0	1	0	1	0	0
28	Alocandrena	0	0	0	0	0	0	0	0	0	0	?	0	1	0	0	0	0	0	1	0	4	2	0	0	1	0	1
29	Protoxaea	0	1	0	1	1	2	0	0	0	0	0	1	1	0	0	0	0	0	1	0	4	0	0	0	0	0	1
30	Dieunomia	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1	2	2	0	0	0	1	1	1
31	Nomia	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	2	2	0	0	0	1	1	1
32	Dufourea	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	4	0	0	0	0	0	3
33	Systropha	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	2	4	0	0	0	0	0	1
34	Corynura	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0	1	2	2	1	0	1	0	0	3
35	Pseudaugochlora	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0	1	2	2	1	0	1	0	0	3
36	Augochlora	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0	1	2	2	1	0	1	0	1	3
37	Halictus	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	1	1	2	1	0	1	0	1	3
38	Nomioides	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	1	0	3
39	Agapostemon	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	2	1	0	1	0	1	3
40	Sphecodes	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	2	1	0	1	0	1	1
41	Conanthalictus	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1	0	4	0	0	0	1	0	3
42	Meganomia	0	1	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	5	0	0	0	1	0	1
43	Macropis	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	4	0	0	0	0	0	3
44	Hesperapis	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	5	0	0	0	1	1	3
45	Dasypoda	0	0	1	0	0	0	2	0	0	0	1	1	1	0	0	0	0	0	1	2	5	0	0	0	0	1	3
46	Melitta	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	2	1	0	0	0	1	0	3
47	Xeralictus	0	0	0	0	0	0	0	0	0	0	?	0	1	0	0	2	0	0	1	2	5	0	0	0	0	0	3
48	Ctenoplectra	0	1	1	0	0	0	0	0	0	0	1	2	1	0	0	0	0	0	1	2	5	2	0	0	0	1	2
49	Neofidelia	1	0	0	1	1	1	0	0	0	0	1	2	0	1	0	0	3	1	1	0	1	0	0	0	0	0	3
50	Pararhophites	0	0	1	1	1	0	0	0	0	0	1	1	0	1	0	0	3	1	1	0	1	0	0	0	0	0	3
51	Lithurge	1	1	1	1	1	1	0	0	0	0	1	2	0	0	0	0	4	0	1	0	2	1	0	0	1	0	2
52	Exomalopsis	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	5	0	0	0	0	0	2
53	Manuella	0	0	0	0	0	0	2	0	0	0	0	0	1	0	0	0	4	0	1	2	2	0	0	1	0	0	2
54	Nomada	0	0	0	0	0	0	2	0	0	0	1	0	1	0	1	0	0	0	1	0	3	0	0	1	0	1	1
55	Triepeolus	0	0	0	0	0	0	2	0	0	0	2	0	0	0	1	0	0	0	1	0	3	0	0	1	0	0	2
56	Haplomelitta	0	0	1	?	0	0	1	0	0	0	1	0	1	0	0	0	0	0	1	2	5	0	0	0	0	0	1
57	Fidelia	1	0	0	1	1	1	0	0	0	0	1	2	0	1	0	0	3	1	1	2	4	0	0	0	1	0	3
58	Aphilanthops	1	0	0	0	0	0	0	1	0	0	2	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
59	Philanthus	1	0	0	0	0	0	0	2	1	0	2	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	1
60	Passaloecus	1	0	1	0	0	0	0	1	1	0	3	0	0	0	0	0	2	0	0	2	0	0	0	0	1	0	0
61	Tachytes	1	0	0	0	0	1	4	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
62	Sphecius	1	0	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0
63	Sphex	0	0	0	0	0	1	3	3	1	1	3	0	0	0	0	0	2	0	0	1	0	1	0	0	1	0	0
64	Astata	1	0	0	0	1	0	4	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
65	Sceliphron	0	0	0	0	0	1	3	3	1	1	3	0	0	0	0	0	2	0	0	1	0	1	0	0	1	0	0

Table 2, continued

		109	53	57	58	110	111	112	113	114
			53a.	57a.	58a.	53b	53c	57b	58b	58c
1	Colletes	0	3	3	3	0	0	0	0	0
2	Caupolicana	0	4	3	3	0	0	0	0	0
3	Leioproctus	0	3	3	3	0	0	0	0	0
4	Callomelitta	0	3	3	3	0	0	0	0	0
5	Scrapter	0	3	3	3	0	0	0	0	0
6	Trichocolletes	0	3	3	3	0	0	0	0	0
7	Lonchopria	0	3	3	3	0	0	0	0	0
8	Eulonchopria	0	3	3	3	0	0	0	0	0
9	Cadeguala	0	4	3	3	0	0	0	0	0
10	Euryglossa	0	3	3	3	0	0	0	0	0
11	Hylaeus	0	3	3	3	0	0	0	0	0
12	Hyleoides	0	3	3	3	0	0	0	0	0
13	Amphylaeus	0	2	3	3	0	0	0	0	0
14	Chilicola	0	3	3	3	0	0	0	0	0
15	Euryglossula	0	3	3	3	0	0	0	0	0
16	Mourecotelles	0	3	3	3	0	0	0	0	0
17	Diphaglossa	0	4	3	3	0	0	0	0	0
18	Meroglossa	0	2	2	2	0	0	0	0	0
19	Crawfordapis	0	4	3	3	0	0	0	0	0
20	Mydrosoma	0	4	3	3	0	0	0	0	0
21	Ctenocolletes	0	?	3	3	0	1	0	0	0
22	Andrena	0	1	1	1	0	0	0	0	0
23	Protandrena	0	1	1	1	0	0	0	0	0
24	Hypomacrotera	0	1	1	1	1	0	0	0	1
25	Pterosarus	0	1	1	1	1	0	0	0	0
26	Euherbella	0	1	1	1	0	0	0	0	0
27	Megandrena	0	1	1	1	0	0	0	0	0
28	Alocandrena	0	1	1	1	0	0	0	0	0
29	Protoxaea	0	1	1	1	0	0	0	0	0
30	Dieunomia	0	1	1	1	0	0	0	0	0
31	Nomia	0	1	1	1	0	0	0	0	0
32	Dufourea	0	1	1	1	0	0	0	0	0
33	Systropha	0	1	1	1	0	0	0	0	0
34	Corynura	0	1	1	1	0	0	0	0	0
35	Pseudaugochlora	0	1	1	1	0	0	1	0	0
36	Augochlora	0	1	1	1	0	0	0	0	0
37	Halictus	0	1	1	1	0	0	0	0	0
38	Nomioides	0	1	1	1	0	0	0	0	0
39	Agapostemon	0	1	1	1	0	0	0	0	0
40	Sphecodes	0	1	1	1	0	0	0	0	0
41	Conanthalictus	0	1	1	1	0	0	0	0	0
42	Meganomia	0	1	1	1	0	0	0	0	0
43	Macropis	0	1	1	1	0	0	0	0	0
44	Hesperapis	0	1	1	1	0	0	0	0	0
45	Dasypoda	0	1	1	1	0	0	0	0	0
46	Melitta	0	1	1	1	0	0	0	0	0
47	Xeralictus	0	1	1	1	0	0	0	0	0
48	Ctenoplectra	1	1	1	1	0	0	0	1	0
49	Neofidelia	0	1	1	1	1	0	1	1	0
50	Pararhophites	0	1	1	1	1	0	1	1	0
51	Lithurge	0	1	1	1	1	0	1	1	0
52	Exomalopsis	1	1	1	1	1	0	1	1	0
53	Manuella	1	1	1	1	1	0	1	1	0
54	Nomada	0	1	1	1	1	0	1	1	0
55	Triepeolus	0	1	1	1	1	0	1	1	0
56	Haplomelitta	0	1	1	1	0	0	0	0	0
57	Fidelia	0	1	1	1	1	0	1	1	0
58	Aphilanthops	0	0	0	0	0	0	0	0	0
59	Philanthus	0	0	0	0	0	0	0	0	0
60	Passaloecus	0	0	0	0	0	0	0	0	0
61	Tachytes	0	0	0	0	0	0	0	0	0
62	Sphecius	0	0	0	0	0	0	0	0	0
63	Sphex	0	0	0	0	0	0	0	0	0
64	Astata	0	0	0	0	0	0	0	0	0
65	Sceliphron	0	0	0	0	0	0	0	0	0

a MacIntosh II), neither PAUP nor Hennig86 can import and operate on a file with this many trees, so that it is not possible to determine the best fit of each character for this set of trees. When each of the smaller sets of trees found by Hennig86 and PAUP is analyzed, the weights assigned to characters are not always the same, and different trees are found to be most parsimonious with these two sets of differently weighted characters. (The thirteen characters that receive different weights are indicated by asterisks in Table 3.) Because successive approximations applied to these incomplete data sets yields partially conflicting results, the inability to apply this weighting procedure to the entire set of most parsimonious trees means that it would be questionable to try to derive phylogenetic conclusions from successive approximations with the Series I data matrix at this time.

Implied Weighting. Analysis of the Series I data matrix with Goloboff's implied weights procedure found four fittest trees with a fit of 600.0 steps. Weights assigned to each character by this procedure are shown in Table 3. Eleven characters did not receive the same weight on all four trees, because they showed less homoplasy on one pair of trees than on the other. Both weights assigned to each of these characters are shown in Table 3.

A strict consensus tree for these four trees (Fig. 6) shows one polytomy in the outgroup and two within the bees: at node J (exemplars of Hylaeinae) and at node R (near the base of the Halictidae.) The available data provide no resolution for the polytomy at node J, but the polytomy at node R can be resolved in two ways that yield a tree with the same total fit. Either *Nomioides* + *Conanthalictus* is a clade that is the sister group of the taxa subtended by node S (hereafter called component S); or *Nomioides* is the sister of component S, and *Conanthalictus* is the sister group of *Nomioides* + component S.

As in the analysis in which all characters receive equal weight, Halictidae (node G) and the MCL-T clade (node H) are supported in the implied weights analysis. The clade Andrenidae + Oxaeidae (node F') is also supported, but in the implied weights analysis this clade does not include Stenotritidae *(Ctenocolletes).* Instead, *Ctenocolletes* is the basal lineage within the bees (node A). Colletidae in the implied weights analysis (node E') include Euryglossinae (node B) and thus correspond to the family as it has traditionally been recognized. Relationships among these families are fully resolved, with the phyletic sequence being Stenotritidae, Colletidae, Halictidae, Andrenidae/Oxaeidae, MCL-T.

Relationships within the larger families are generally well resolved. As in the analysis with equal weighting, monophyletic groups corresponding to recognized subfamilies within Colletidae include Diphaglossinae (node I, Fig. 6), Hylaeinae (node J),

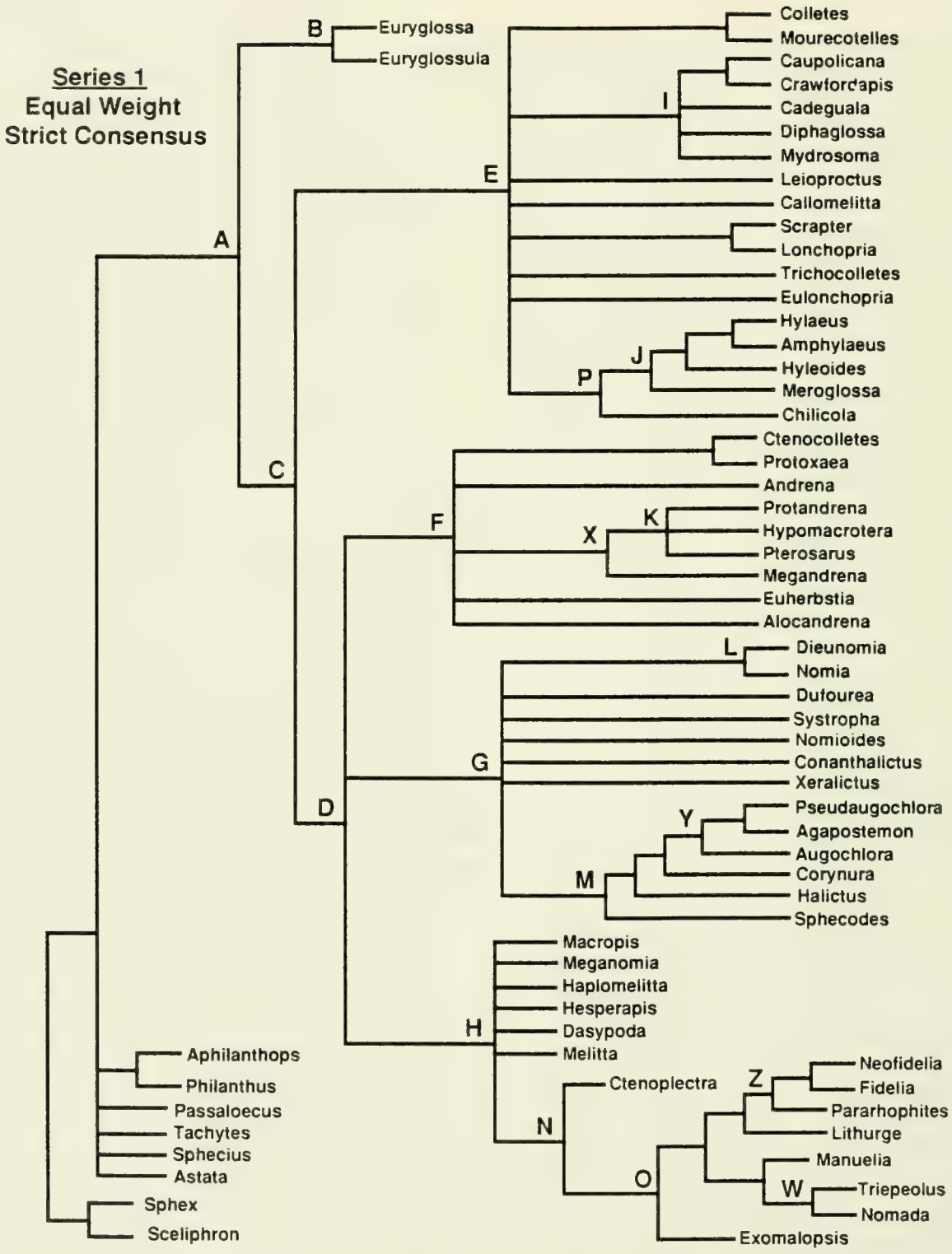


Fig. 5. Strict consensus tree for 4,296 trees found by NONA in Series I analyses using exemplars and equal weighting for all characters. Analyses using PAUP and Hennig86 exceeded memory buffer before all trees could be stored, but yielded the same strict consensus tree; see text for details.

Char	H86	PAU	IW	Char	H86	PAU	IW	Char	H86	PAU	IW	Char	H86	PAU	IW
1	10	10	10.0	**29**	3	3	7.5	**57**	7	7	7.5	**85**	1	1	4.2
2	0	0	5.0	***30**	0	1	6.0	**58**	10	10	10.0	**86**	1	1	5.0
3	0	0	1.5	**31**	10	10	7.5, 10.0	**59**	10	10	10.0	**87**	0	0	2.3, 2.5
4	10	10	10.0	**32**	2	2	6.0	**60**	2	2	3.3	***88**	1	2	3.7
5	0	0	2.1	**33**	3	3	5.0	**61**	10	10	10.0	**89**	6	6	7.5
6	10	10	10.0	**34**	10	10	10.0	**62**	1	1	4.2, 5.0	**90**	4	4	7.5
7	1	1	1.3	**35**	6	6	6.0, 7.5	**63**	1	1	2.3	**91**	10	10	10.0
8	0	0	1.4	**36**	10	10	10.0	**64**	0	0	1.6	**92**	0	0	1.5
9	10	10	10.0	***37**	1	2	3.0	**65**	0	0	2.3	**93**	0	0	1.6
10	0	0	1.6	**38**	2	2	3.0	**66**	0	0	1.7	**94**	2	2	4.2
11	2	2	5.0	**39**	2	2	2.5, 2.7	**67**	0	0	3.7	**95**	10	10	10.0
12	1	1	1.7	**40**	1	1	3.3	**68**	2	2	6.0	**96**	10	10	10.0
***13**	0	1	3.3	**41**	1	1	1.6, 1.7	**69**	10	10	10.0	**97**	2	2	7.5
***14**	10	4	10.0	**42**	1	1	5.0	**70**	2	2	6.0	***98**	4	3	3.7
15	3	3	5.0	**43**	1	1	6.0	**71**	4	4	7.5	**99**	10	10	10.0
16	0	0	2.7	**44**	2	2	6.0	**72**	1	1	2.5	**100**	10	10	10.0
17	1	1	1.8	**45**	3	3	10.0	**73**	1	1	2.3	**101**	0	0	1.3 1.4
18	1	1	2.0	**46**	3	3	5.0	**74**	4	4	7.5	***102**	3	2	2.5
19	1	1	3.0	**47**	3	3	6.0, 7.5	**75**	0	0	3.0	***103**	1	2	4.2
20	2	2	6.0	**48**	4	4	7.5	**76**	10	10	10.0	**104**	10	10	10.0
21	1	1	3.0, 3.3	***49**	0	1	3.7	**77**	2	2	7.5, 10.0	***105**	1	2	4.2
22	0	0	1.7	**50**	0	0	4.2	**78**	0	0	3.7	**106**	0	0	1.3 1.4
23	10	10	10.0	**51**	1	1	6.0	***79**	1	0	2.5	**107**	0	0	3.7
24	2	2	7.5	**52**	5	5	7.5	**80**	10	10	10.0	**108**	0	0	1.5
***25**	2	1	5.0	**53**	8	8	7.5	**81**	10	10	10.0	**109**	0	0	7.5
26	2	2	6.0	***54**	5	4	6.0	**82**	1	1	5.0				
27	2	2	3.0	**55**	4	4	6.0	**83**	0	0	5.0				
28	4	4	7.5	**56**	4	4	7.5	**84**	0	0	2.7				

Table 3. FINAL WEIGHTS ASSIGNED TO CHARACTERS BY SUCCESSIVE APPROXIMATIONS WEIGHTING IN TWO SETS OF ANALYSES AND BY IMPLICIT WEIGHTING IN SERIES I, PART 1. The column labeled **Char** lists the number of the character as used in Table 2, Figures 7 and 9, and as described in the text. The column labeled **H86** shows weights based on files of more than 2,000 trees from analyses using the Hennig86 program; the column labeled **PAU** shows weights based on a file of 500 trees from an analysis using the PAUP program (see text for details). The column labeled **IW** shows weights assigned by implied weighting as implemented by the program PeeWee. Both weights are shown for characters that received more than one weight with this procedure. Characters marked with an asterisk received different weights in the H86 and PAUP analyses.

and Euryglossinae (node B). Xeromelissinae are represented by only one exemplar *(Chilicola)*, so our study sheds no light on the monophyly of this group. Colletinae are polyphyletic, with *Scrapter* the sister taxon of *Chilicola* + Hylaeinae, and the remaining exemplars in our study forming an assemblage that is paraphyletic with respect to Diphaglossinae. Within this assemblage, the clade *Colletes* + *Mourecotelles* corresponds to the tribe Colletini of Michener (1989). The remaining exemplars correspond to the tribe Paracolletini, which is paraphyletic with respect to Colletini; recent works (Michener, 1992, etc.) have ignored the 1989 tribal classification as untenable. The results of this implied weights analysis are consistent with Michener's (1986) partitioning of Diphaglossinae into the tribes Caupolicanini (exemplars: *Caupolicana, Crawfordapis*), Diphaglossini (exemplars: *Cadeguala, Diphaglossa*), and Dissoglottini (exemplar: *Mydrosoma*), although the relationships among these tribes are not as hypothesized by Michener.

Within Andrenidae, Panurginae (node K) are monophyletic, as in the analysis with equal weighting. The remaining andrenid genera are exemplars of

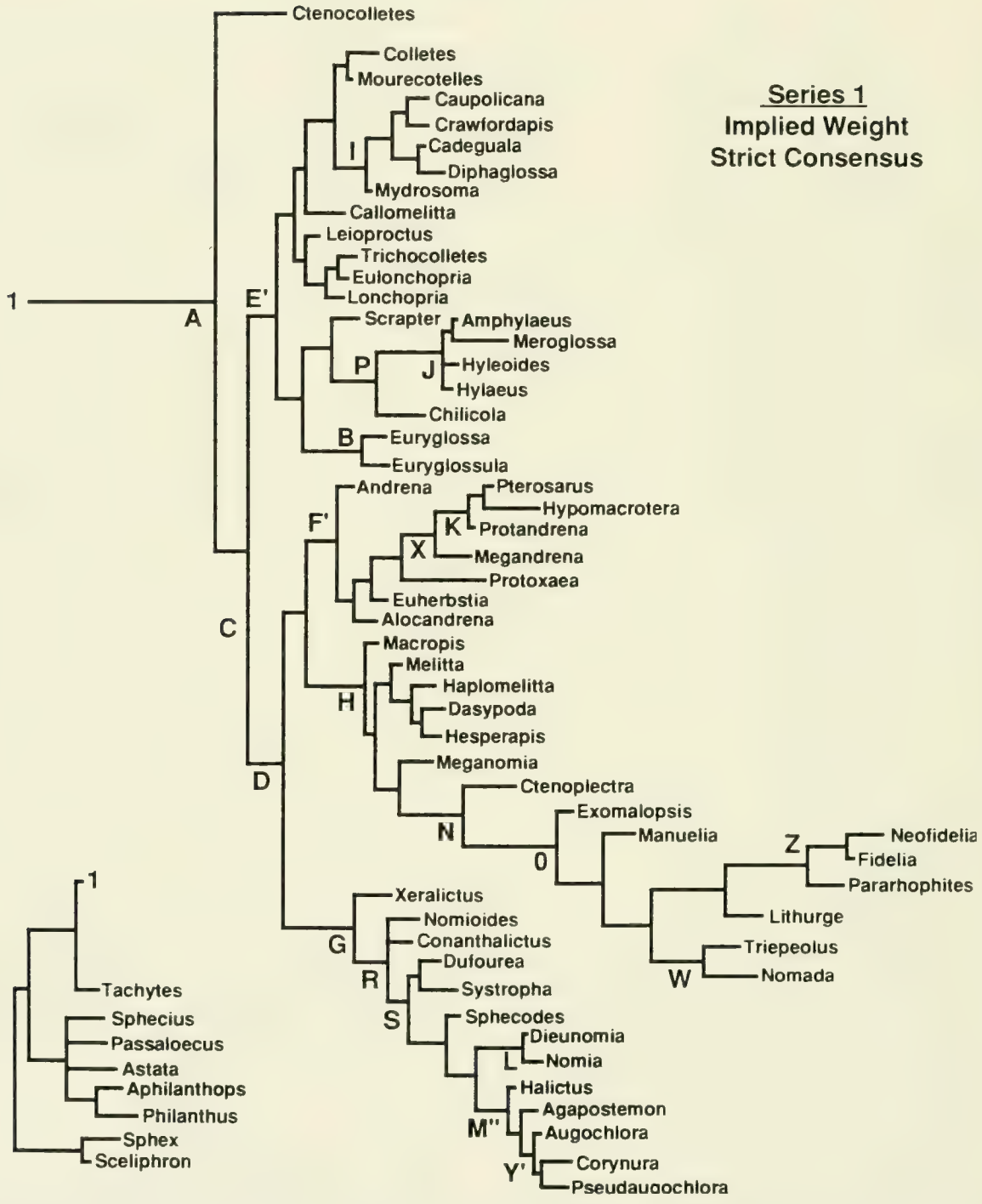


Fig. 6. Strict consensus tree for 4 trees from Series I analyses using exemplars and implied weights. Branch lengths are proportional to the weighted number of characters along each branch.

Andreninae, which is a polyphyletic assemblage. *Megandrena* is the sister of Panurginae, and the remaining three genera are paraphyletic with respect to this clade and *Protoxaea*.

Within Halictidae, despite the fact that implied weighting achieved much more complete resolution than equal weighting, the conclusions regarding subfamilies are nearly the same (Fig. 6). Only Nomiinae

are monophyletic, and both *Nomioides* and *Sphecodes* are outside the clade that includes the rest of our exemplars of Halictinae (node M" on Fig. 6). Within this more narrowly defined Halictinae, Halictini (represented by *Halictus* and *Agapostemon*) are paraphyletic with respect to Augochlorini (node Y'). Rophitinae including *Nomioides* are a polyphyletic assemblage of genera at the base of the Halictidae.

Although our exemplars of Melittidae form a group that is paraphyletic with respect to L-T bees, the implied weights analysis partitions them into three distinct groups that can be compared to the subfamilies recognized by Michener (1981a). Our three exemplars of Dasypodinae (*Haplomelitta, Dasypoda,* and *Hesperapis*) form a monophyletic group. Melittinae, represented by *Melitta* and *Macropis,* do not form a monophyletic group, but evidence for their monophyly in Michener's earlier study was a single character that also occurs in Dasypodinae and whose polarity was considered equivocal (Michener, 1981a, figs. 1, 2). *Meganomia* is our sole exemplar of Meganomiinae, so the monophyly of this subfamily is not tested in our study. (Michener's 1981 study found 13 autapomorphies for this subfamily, so its monophyly seems well supported.)

Series I, Part 2: Analyses Based on Family Groundplans

In all the preceding analyses, the majority of characters exhibit homoplasy, but much of this homoplasy occurs sporadically within major clades that more or less correspond to presently recognized families. If one is primarily interested in determining the phylogenetic relationships among these major clades, the informative characters are those that vary between these clades. Synapomorphies shared by the ancestors of these clades provide evidence of phylogenetic relationships among the clades, and subsequent character evolution within each clade is of secondary interest.

The analyses described in Part 1 provide a basis for hypothesizing the groundplan of each major clade. Such groundplans can be used to construct a smaller data matrix in which each major clade is represented by a single terminal "taxon." Analysis of this matrix can then focus on patterns of character variation among, rather than within, the major clades of S-T bees. With a smaller matrix, it is also feasible to do exact rather than approximate searches for the most parsimonious trees.

Because the analyses described in Part 1 produce a number of different phylogenetic hypotheses, several different hypothetical groundplans could be constructed for each major clade. We present analyses based upon two different sets of groundplans, one derived from the analysis in which all characters received equal weight, the other derived from the analysis using implied weights. In each case, we used Maddison and Maddison's (1992) MacClade program to optimize the distribution of each character on a strict consensus tree and thus infer the character state present in the ancestor of any clade of interest. Although a strict consensus tree is not generally the best overall hypothesis of phylogenetic relationships, it can call attention to characters for which ancestral states are equivocal, and it is useful to be aware of such uncertainty in an analysis based upon hypothetical groundplans.

In all of our analyses in Part 1 that give equal weight to each character, the same strict consensus tree is found (Fig. 5); in the following discussion, we refer to groundplans derived from this tree as *EQWT (for "equal weight") groundplans.* Groundplans derived from the strict consensus tree found in the implied weights analysis (Fig. 6) will be called *IW groundplans.* Table 4 shows the character and state codes for two groundplans.

Each groundplan analysis used a matrix with eight taxa: a hypothetical ancestor of all bees (Urbiene), used to root the tree, and seven terminal taxa that are either hypothetical ancestors of monophyletic groups of bees present on all strict consensus trees or sole exemplars (in our study) of traditionally recognized families of S-T bees. These seven ingroup taxa are: (1) *Ctenocolletes* (exemplar of Stenotritidae); (2) *Protoxaea* (exemplar of Oxaeidae); (3) Euryglossinae (common ancestor of *Euryglossa* + *Euryglossula,* node B in Figs. 5 and 6); (4) Colletidae (common ancestor of the other 18 colletid genera in our study, subtended by node E or E' in Figs. 5 and 6); (5) Halictidae (common ancestor of all genera subtended by node G in Figs. 5 and 6); (6) Andrenidae (common ancestor of all genera subtended by node F or F' in Figs. 5 and 6—note that this clade always includes *Protoxaea* and sometimes *Ctenocolletes* in Part 1); and (7) MCL-T clade (common ancestor of all taxa subtended by node H in Figs. 5 and 6).

All analyses with each of these data matrices employed exact searches with PAUP's branch-and-bound algorithm. Only informative characters were used in calculating L, ci, and ri, and only these characters are shown on the cladograms. An "informative" character is one that can potentially provide information about phylogenetic relationships, which means that more than one state must be present in the ingroup, and each of these states must be shared by two or more taxa. (With a multistate character, some states may be autapomorphies found only in one taxon, but if there are no states shared by two or more taxa, the character is uninformative unless an ordered transformation series is specified *a priori.*)

EQWT Groundplans. This analysis is based upon 31 informative characters (Tables 4 and 5). With all

Character	Ancestor (Urbiene)	Ctenocolletes	Protoxaea	Andrenidae	Colletidae	Halictidae	Melittidae + L-T Bees	Euryglossinae
1	1	1	1	1	1	1	1	1
2	0	1	1	0	0	0	0	0
3	0	1	1	0/1/2 (1)	0	0/1/2 (0)	0	0
4	0	1	2	0/2 (2)	0	0	0	0
5	0	0	0	0	0/1 (0)	0	0	0
6	1	1	1	1	1	1	1	1
7	0/1/4	1	1	1/3/4	0/1/4	0/1	0/1	4
8	0	0	2	0/1 (1)	0	0 (1)	0/1 (1)	0
9	1	1	1	1	1	1	1	1
10	0	0	2	0	0	0	0	0
11	0	0	1	0	0	0	0	0
12	3 (2/3)	3	1	3	2/3	3 (2/3)	3	3
13	1	1	1	1	1	1	1	1
14	0	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0/1 (1)	0
16	0	0	2	0	0	0	0	0
17	0 (0/1/2)	2	2	2	2	2 (0)	2	0
18	1 (0)	0	0	0	0	0 (3)	0	1
19	0	0	1	1	0	2	1	0
20	1	1	0	1	1	1	1	1
21	0	0	0	0	0	0	0	0
22	0/1 (1)	1	1	1 (0/1)	1	2	1 (0)	0/1 (1)
23	1	1	1	1	1	1	1	1
24	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	0
26	1	1	1	1	1	1	1	1
27	1	1	1	1	1	1	1	1
28	0	0	0	0	0	1	0	0
29	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0
31	1	1	1	1	1	1	1	1
32	0/1 (1)	1	1	1	1	1	1	0
33	0	0	2	0	0	0	0	0
34	0	0	0	0	0	1	0	0
35	0	0	0	0	0	2	0	1
36	0	0	0	0	0	0	0	0
37	0/1 (0)	0	0	0/1 (1)	0/1 (1)	1	1/2 (2)	0/1 (1)
38	0	1	0	1	0	0	1/2 (2)	0
39	2	2	3	2	2	2	1/2 (1)	2
40	0	0	0	0/1	0	0	0/1 (1)	0
41	2	2	1	2	2	1	1/2 (2)	2
42	0	0	0	0/1 (1)	0	0	0/1 (1)	0
43	1	1	1	1	1	1	1	1
44	0 (1)	1	1	1	1	1	1	0
45	0	0	0	0	0	0	0	1
46	0	0	0	0	0	0	0	0/1/3
47	0	0	0	0	0	0	0	0
48	0	0	0	0	0	0	0	0
49	0	0	1	0	0	0	0	0
50	0	0	0	0	0	0	0	0
51	0	0	0	0	0	0	0	0
52	0	0	0	0	0	0	0	0
53	0	5	1	1	0	1	1	0
54	0/3 (0)	2	0	0	3	0/1 (0)	0	3
55	0	0	0	0	2 (0)	0	0	0
56	0	0	0	0	0	0	0	1
57	0	0	1	1	0	1	1	0

Table 4. DATA MATRICES FOR THE ANALYSES IN SERIES I, PART 2, IN WHICH TERMINAL TAXA REPRESENT HYPOTHETICAL FAMILY GROUNDPLANS. "Urbiene" refers to the hypothetical ancestor of all bees. The complete matrix for EQWT groundplans (as defined in the text) is shown at the left of each column; only character states that differ from this matrix are shown (in parentheses) for the IW groundplan matrix. A "/" between character states indicates that any of the states listed is equally likely to have been present in the groundplan.

Table 4, continued

Character	Ancestor (Urbiene)	Ctenocolletes	Protoxaea	Andrenidae	Colletidae	Halictidae	Melittidae + L-T Bees	Euryglossinae
58	0	0	2	2	0	2	2	0
59	0	0	0	0	0	0	0	0
60	0	0	0	0	0	0	0	0
61	0	0	0	0	1	0	0	1
62	0	0	0	0	0	0	0/1 (1)	0
63	0 (0/1)	1	3	1	0	0/1	1 (2)	0
64	0	1	1	0	0/1 (0)	0 (0/1)	0	0
65	0	2	2	0/2 (0)	0	0	0/1/2 (2)	0
66	0 (1)	1	1	0/1 (1)	0 (1)	0	0/1 (1)	0 (1)
67	0	0	0	0	0	0	0	0
68	1	1	1	1	1	1	1	1
69	1	1	1	1	1	1	1	1
70	1	1	1	1	1	1	1	1
71	1	1	1	1	1	1	0/1 (0)	1
72	0 (2)	2	2	1/2 (2)	2	2	1/2 (1)	0
73	0/1 (1)	1	1	1	0/1 (1)	1	0/1 (1)	1
74	1	1	1	1	1	1	1	1
75	0	1	0	0	0	0	0	0
76	0	0	0	0	0	0	0	0
77	1	1	1	1	1	1	1	1
78	0	2	0	0	0	0	0	0
79	0 (0/1)	1	1	1	0	1/2 (1)	0/1 (1)	0
80	1	1	1	1	1	1	1	1
81	1	1	1	1	1	1	1	1
82	0	0	0	0	0	0	0	0
83	0	0	1	0	0	0	0	0
84	0	0	0	0	0	0	0	1
85	0	1	1	0	0	0	0	0
86	0	0	1	0	0	0	0	0
87	0 (1)	1	2	0	0	0	0	0
88	0	0	0	0	0	0	0	0
89	0	0	0	0	0	0	0	0
90	0	0	0	0	0	0	0	0
91	0	0	0	0	0	0	0	0
92	1	2	0	1	0/1 (1)	1	1	1
93	0	0	1	0	0	0	0	0
94	0/1 (1)	1	1	1	0/1 (1)	1	1	1
95	0	0	0	0	0	0	0	0
96	0	0	0	0	0	0	0	0
97	0	0	0	0	0	0	0	0
98	0/2 (0)	0	0	0	0/2 (0)	0	0	0
99	0	0	0	0	0	0	0	0
100	1	1	1	1	1	1	1	1
101	2 (0)	0	0	2 (0)	2	2 (0)	2 (0)	2
102	4 (0)	0	4	4	4	2/4 (4)	4	4
103	0	0	0	0	0	0	0	0
104	0	0	0	0	0	0	0	0
105	0	0	0	0	0	0	0	0
106	1 (0)	0	0	1	1 (0)	1 (0)	1 (0)	1 (0)
107	0	0	0	0	0	0/1 (0)	0/1 (0)	0
108	0/3 (1)	1	1	1/3 (3)	0/1/3 (3)	1/3 (3)	1/3 (3)	0/3 (3)
109	0	0	0	0	0	0	0	0

characters given equal weight, there are five minimum length trees, with L = 69, ci = 0.91, ri = 0.83, as shown in Figure 7. Figure 8 is the strict consensus tree for these five trees. This result was stable to successive and implied weighting, i.e., the same five trees were the optimal solution (shortest or fittest trees) when these weighting procedures were used. A common feature of these trees and the analyses in Part I that weighted all characters equally is that Euryglossinae were the basal clade of bees, followed by the rest of the Colletidae. *Ctenocolletes* and *Protoxaea* were also sister taxa in all five trees, but these two were not necessarily more closely related to Andrenidae than to Halictidae or the MCL-T clade.

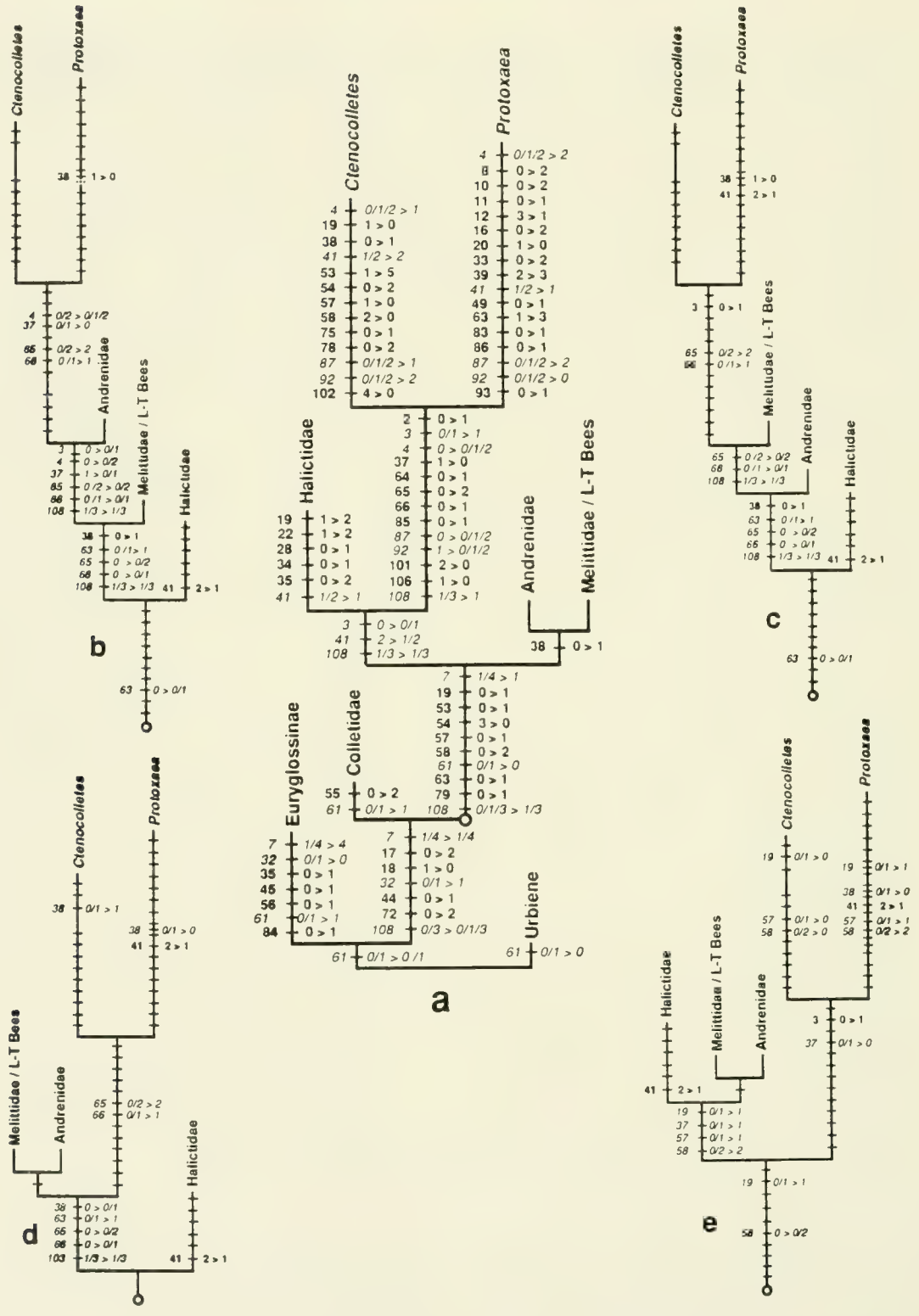


Fig. 7. The five most parsimonious trees found in Series I analyses using EQWT groundplans, as explained in text. Tree designated as *a* shows all taxa, whereas trees *b-e* show only taxa whose placement differs from tree *a*. Urbiene is a hypothetical ancestor used to root the tree.

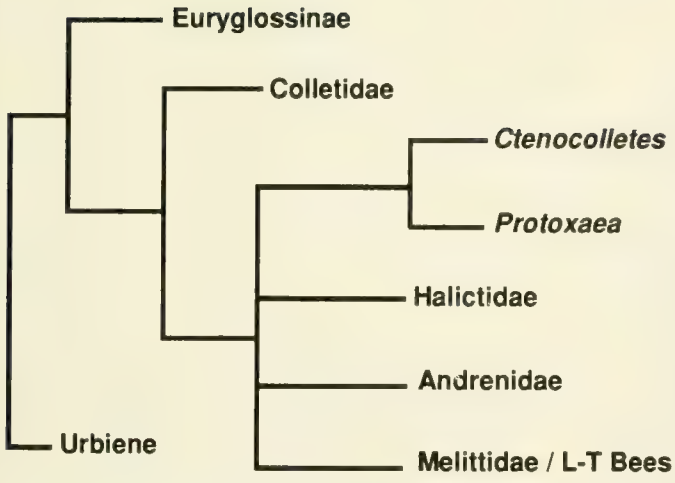


Fig. 8. Strict consensus tree for the five trees shown in Figure 7.

Char	EQW	IW	Char	EQW	IW
2	10	0	**58**	3	10
3	10	0	**61**	0	10
4	10	0	**63**	10	10
7	10	10	**64**	10	0
8	--	10	**65**	10	0
12	--	10	**66**	10	--
17	10	0	**72**	10	--
18	10	--	**73**	10	--
19	4	10	**79**	10	10
22	10	10	**85**	10	0
28	--	--	**87**	--	10
37	10	3	**92**	10	--
38	2	3	**98**	10	--
41	0	10	**101**	10	10
42	--	10	**102**	--	10
44	10	--	**106**	10	--
53	10	10	**107**	10	--
54	10	10	**108**	10	2
57	3	10			

Table 5. FINAL WEIGHTS ASSIGNED TO INFORMATIVE CHARACTERS BY SUCCESSIVE APPROXIMATIONS IN THE TWO GROUNDPLAN ANALYSES IN SERIES I, PART 2. The column labeled **Char** gives the number of each character as in Table 2. Columns labeled **EQW** and **IW** refer to analyses based on family groundplans with those designations (see text and Table 4 for details). A "--" in a column means that the character is uninformative in that data matrix.

(Fig. 7 summarizes the characters supporting the various arrangements.)

IW Groundplans. This analysis was based upon 27 informative characters (Tables 4 and 5). With all characters given equal weight, there were two equally parsimonious trees, with L = 87, ci = 0.85, ri = 0.67 (Fig. 9). Both of these trees were also most parsimonious after successive weighting, and implied weighting selected one of them (p. 404) as the fittest tree, with fit = 210.5.

A common feature of the IW groundplan trees that differs from the EQWT groundplan trees is that the former show Euryglossinae to belong within a clade with the rest of the Colletidae. In the IW groundplan trees, either *Ctenocolletes* (Fig. 9, p. 404) or *Ctenocolletes* + *Protoxaea* (Fig. 9, p. 405) is the basal lineage of bees. In the tree where *Protoxaea* is not the sister group of *Ctenocolletes,* it is sister of Halictidae; i.e., it is not most closely related to Andrenidae in either groundplan tree. Apart from the variable placement of *Protoxaea,* arrangements among the families of bees in the IW groundplan analysis are consistent with those from the analysis using implied weights in Part 1: i.e., the phyletic sequence (excluding *Protoxaea*) is *Ctenocolletes,* Colletidae s.l., Halictidae, Andrenidae s. str., MCL-T.

SERIES II, PART 1: ANALYSES USING EXEMPLARS

Equal Weighting. This analysis employed 65 taxa and 114 characters; the data matrix is shown in Table 2. As explained above (see Methods of Analysis), with a matrix of this size we had to perform approximate searches. There are at least two different islands of equally parsimonious trees, with L = 720, ci = 0.27, ri = 0.69. Following Maddison (1991), these islands will be designated according to the number of trees they contain.

Island-226 (Fig. 10), found by Hennig86, has Halictidae (node G) as the basal lineage of bees. The rest of the bees form two large clades: (1) Andrenidae (including the oxaeid *Protoxaea*) + the MCL-T clade, and (2) a clade that comprises all the Colletidae but also has the stenotritid *Ctenocolletes* imbedded within the colletids, as the sister group of Diphaglossinae (node I').

The size of the second island, I-336, is somewhat more problematic. Searches by PAUP found an island with 84 trees, summarized by the strict consensus tree in Figure 11; whereas searches by NONA found an island with 336 trees, summarized by the strict consensus tree in Figure 12. The consensus trees for the two islands are identical except in Halictidae (node G), where island-336 (Fig. 12) shows a large polytomy that is completely resolved for island-84 (Fig. 11). Because the resolution in Figure 11 is fully consistent with Figure 12, we suspect that NONA's superior ability to locate minimum-length trees enabled it to find alternative resolutions within Halictidae that were not located in our searches with PAUP.

In any case, the common topology of Figures 11 and 12 is quite different from that of Figure 10 (I-226). In the former trees, the MCL-T clade (node H)

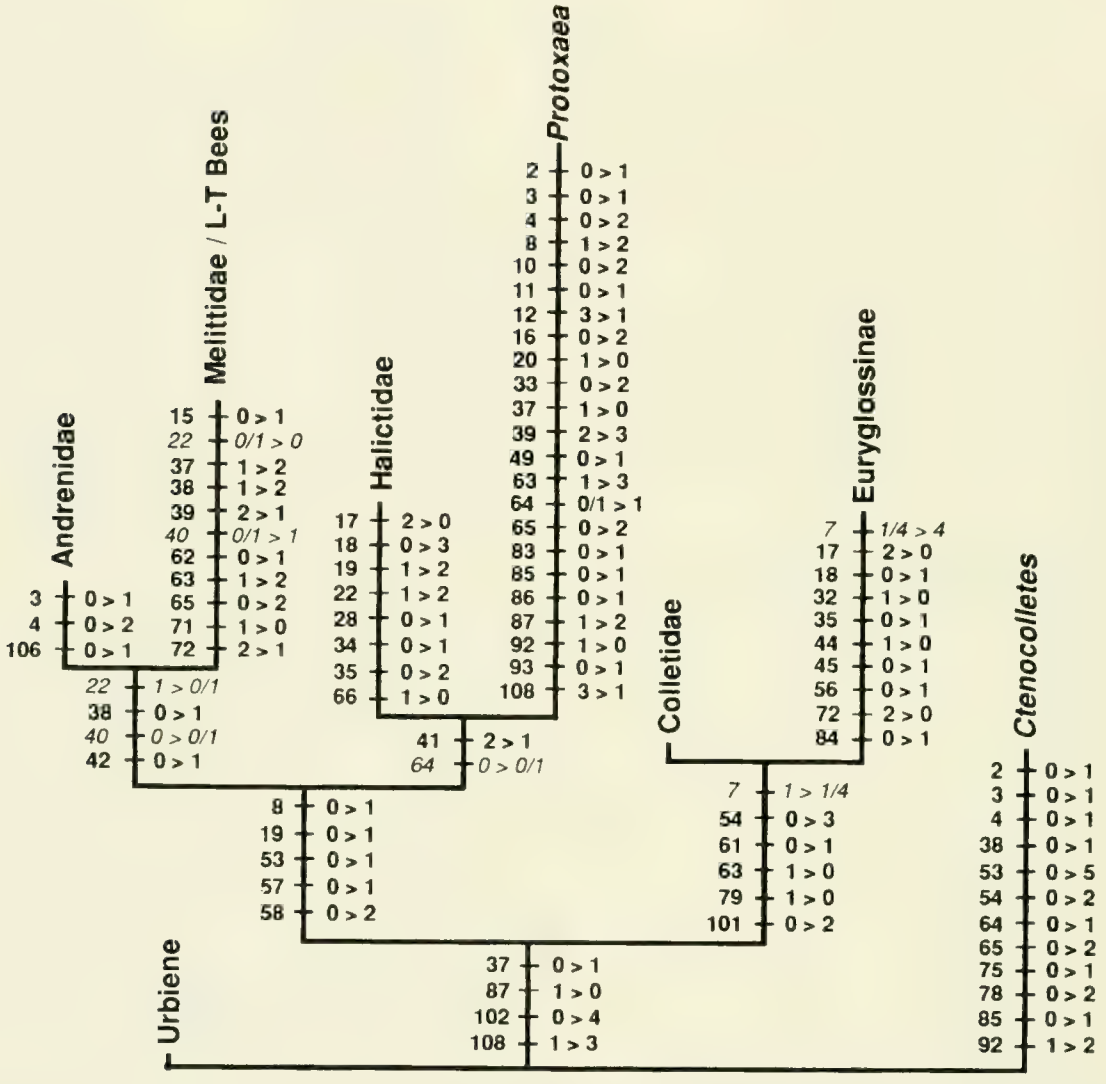


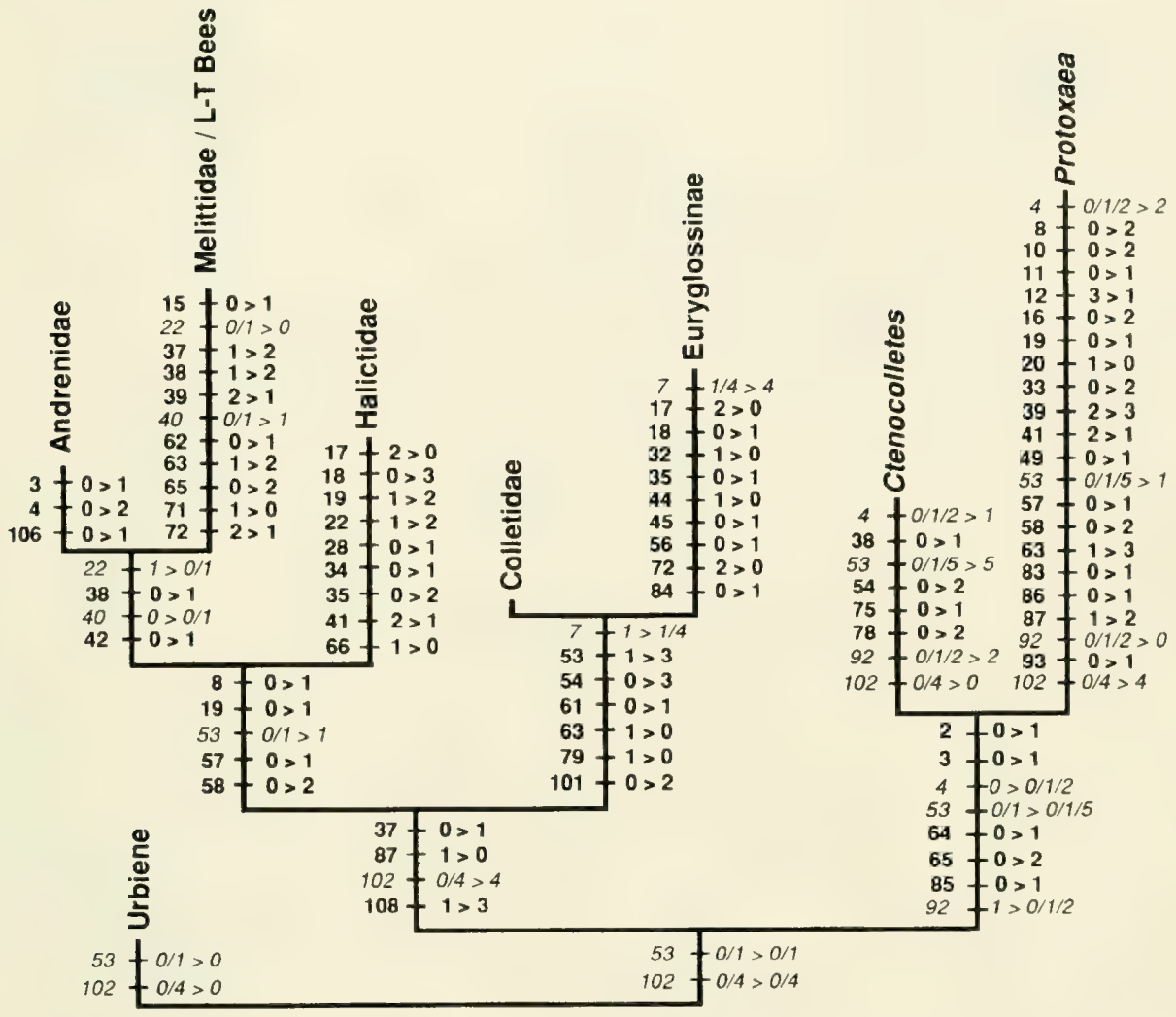
Fig. 9. Trees from Series I analyses using IW groundplans, as explained in text. Tree on lefthand page is the single fittest tree when implicit weighting is applied; the trees are equally parsimonious when successive approximations weighting is used.

is the basal lineage of bees, followed by the phyletic sequence Halictidae (node G), Andrenidae (including *Protoxaea*) (node F'), Stenotritidae *(Ctenocolletes),* and Colletidae (nodes E + B).

A noteworthy common feature of all these trees is that Colletidae are not a basal lineage within the bees, but are one of the most derived lineages. Conversely, the MCL-T clade and Halictidae are the oldest two major groups of bees. Despite these basic disagreements between Series I and Series II concerning the phylogenetic positions of families, the basic composition of these families is fundamentally the same, except that in island-226 the Stenotritidae are imbedded within the Colletidae.

Successive Approximations Weighting. With initial weights assigned according to the best fit of each character to I-226, weights (shown in Table 6) stabilized after five iterations. There were 14 trees, with L = 1037, ci = 0.58, ri = 0.90. The strict consensus tree (Fig. 13) has a very different topology from the consensus tree for the analysis in which all characters received equal weight (Fig. 10). On the other hand, this consensus tree from the successive approximations analysis has the same arrangement of family

Fig. 9, continued



groups as the consensus tree for the island found by PAUP and NONA when all characters were given equal weight (Figs. 11, 12): the MCL-T clade (node H) is the oldest lineage of bees (node H), followed successively by Halictidae (node G), Andrenidae + Oxaeidae (node F'), *Ctenocolletes,* and Colletidae (including Euryglossinae; node E''). However, there are several differences in the way genera are grouped within the families in Figures 11 and 12 as compared to Figure 13.

When initial weights were assigned according to the best fit of each character to the I-336 trees found in the NONA analysis, weights (Table 6) stabilized after 5 iterations, and there were 206 trees with L = 1046, ci = 0.59, ri = 0.90. The strict consensus tree for these 206 trees is shown in Figure 14.

The corresponding analysis applied to the island of 84 trees found by PAUP produced very similar results. Weights (Table 6) stabilized after 4 iterations, and there were 416 trees with L = 1054, ci = 0.59, ri = 0.90. Only 5 of the 114 characters received different weights in these two analyses, and in each case the difference was only one step (Table 6). There are only three differences between the strict consensus tree from this analysis and that in Figure 14, and only one of these concerns the S-T bees: (1) within the L-T bees, *Exomalopsis* is the basal lineage of L-T bees rather than the sister of *Manuelia* + the Megachilidae; (2) within the L-T bees at node Z', the positions of *Pararhophites* and *Neofidelia* are switched; and (3) within Andrenidae, *Andrena* is not the sister group of the genera subtended by node X, but is part of a polytomy at F''.

A consistent result of all Series II analyses using successive approximations weighting is that the phylogenetic sequence of family groups has MCL-T bees

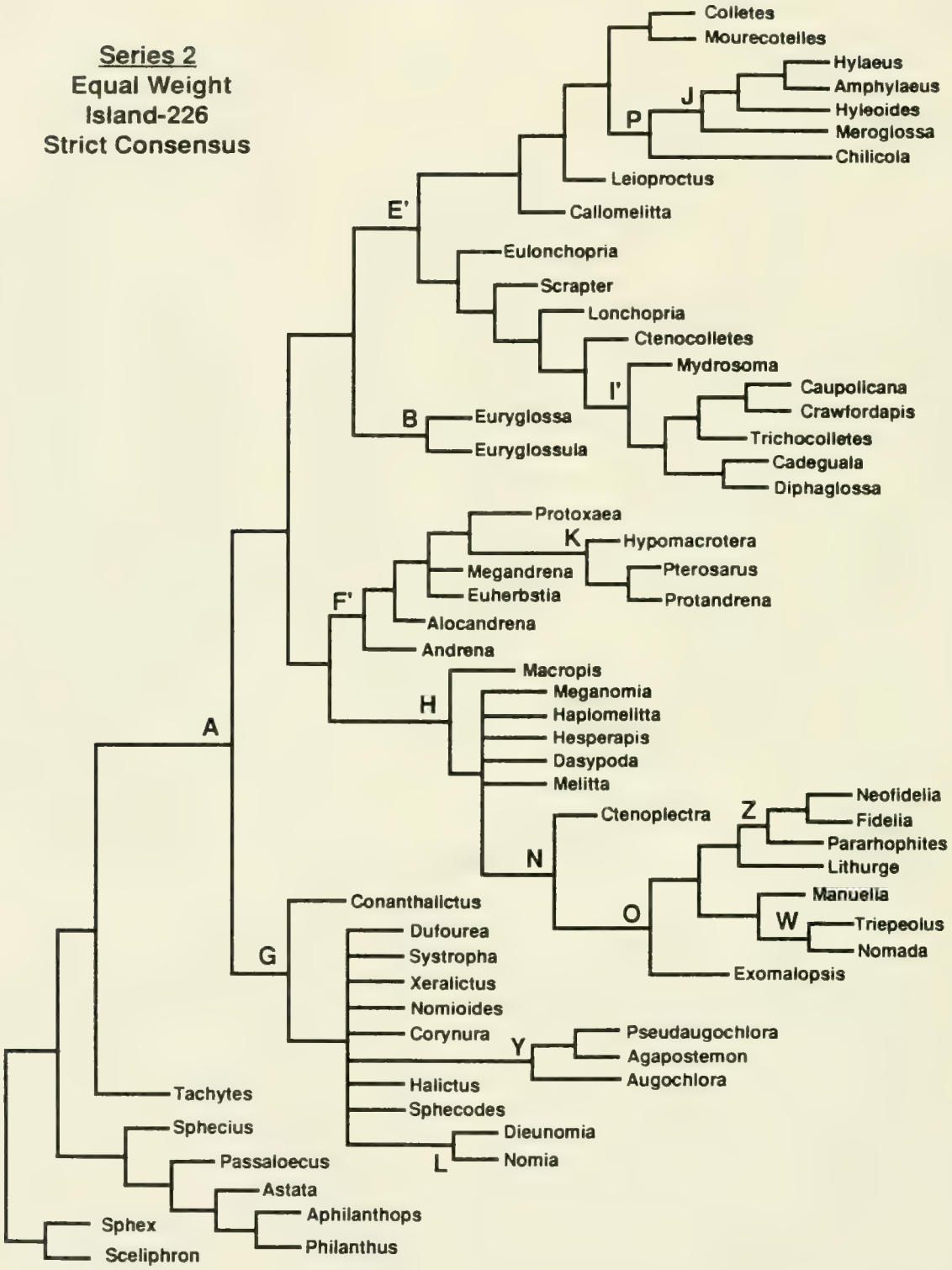


Fig. 10. Strict consensus tree for island-226 from the Series II analysis using exemplars and equal weighting for all characters.

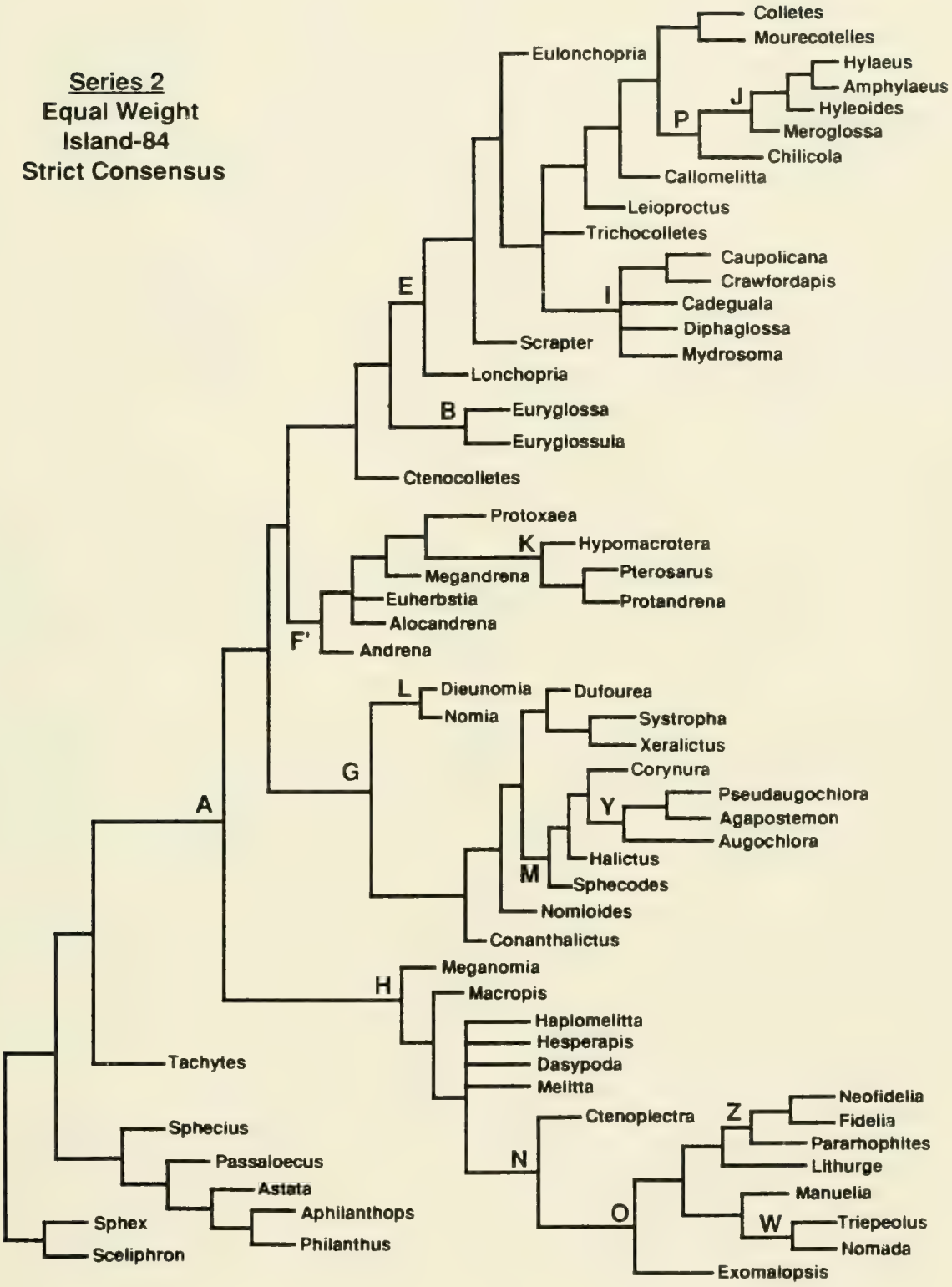


Fig. 11. Strict consensus tree for an island of 84 trees found by PAUP in the Series II analysis using exemplars and equal weighting for all characters. See text for discussion of this tree and Figure 12.

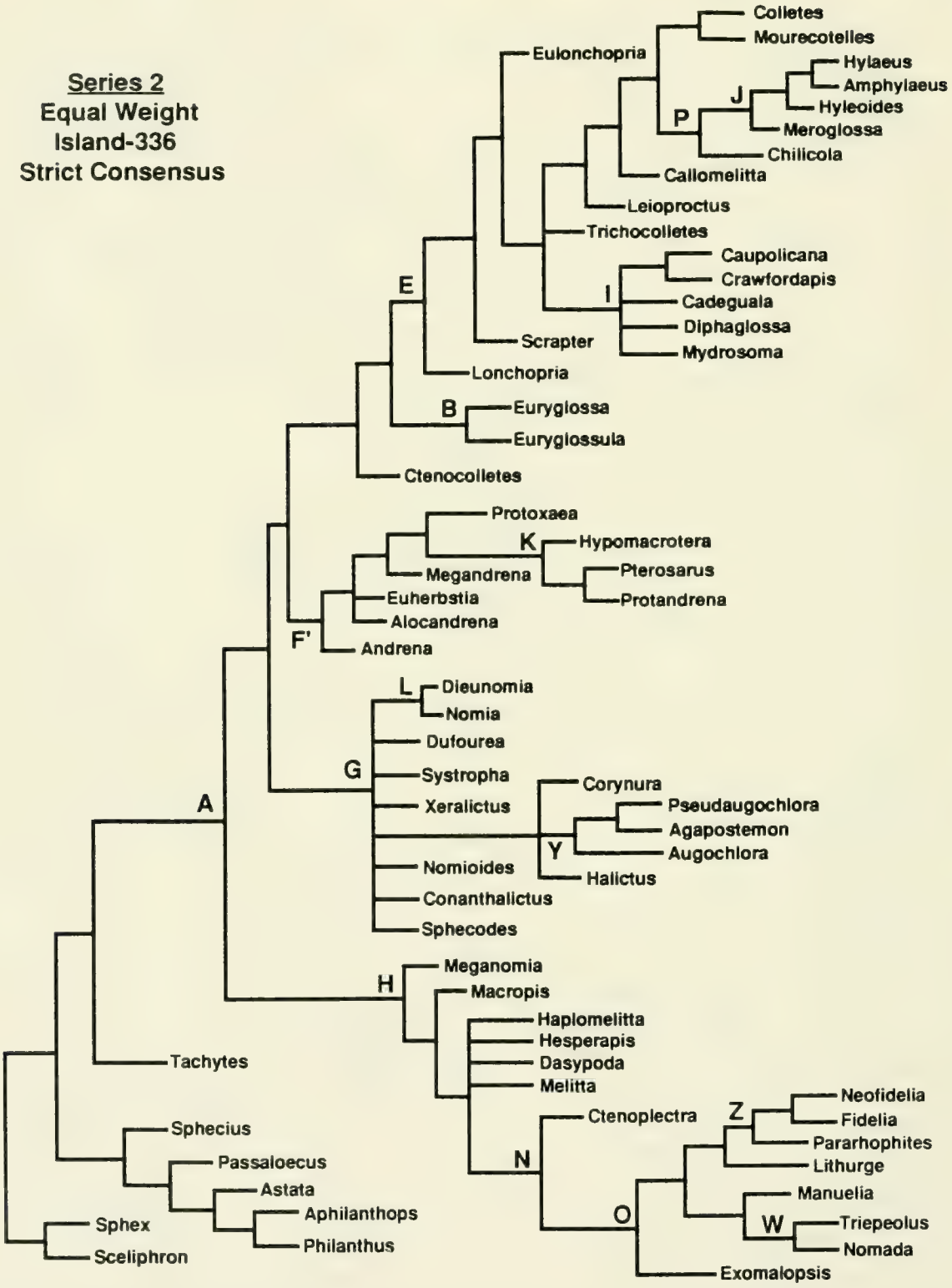


Fig. 12 Strict consensus tree for an island of 336 trees found by NONA in the Series II analysis using exemplars and equal weighting for all characters.

Char	226	336	IW	Char	226	336	IW	Char	226	336	IW	Char	226	336	IW
1	10	10	10.0	29	3	3	7.5	57	7	7	7.5	85	1	1	4.2
2	0	0	5.0	*30	0	1	6.0	58	7	7	7.5	86	1	1	5.0
3	0	0	1.5	31	10	10	7.5	59	10	10	10.0	87	0	0	2.1
4	10	10	10.0	32	2	2	6.0	60	2	2	3.3	88	2	2	3.7
5	0	0	2.1	33	3	3	5.0	61	10	10	10.0	89	6	6	7.5
6	10	10	10.0	34	10	10	10.0	62	1	1	5.0	90	4	4	7.5
7	1	1	1.4	35	6	6	7.5	63	2	2	2.3	91	10	10	10.0
8	0	0	1.3	36	10	10	10.0	64	0	0	1.6	92	0	0	1.5
9	10	10	10.0	37	1	1	2.7	65	0	0	2.3	93	0	0	1.6
10	0	0	1.6	*38	2	1	2.7	66	0	0	1.7	94	1	1	4.2
11	2	2	5.0	39	2	2	2.3	67	0	0	3.3	95	10	10	10.0
12	1	1	1.7	40	1	1	3.7	68	2	2	6.0	96	10	10	10.0
*13	0	1	4.2	41	1	1	1.6	69	10	10	10.0	97	2	2	7.5
14	10	10	10.0	42	1	1	4.2	70	2	2	6.0	98	2	2	3.7
15	3	3	5.0	43	1	1	6.0	71	10	10	10.0	99	10	10	10.0
16	0	0	2.5	44	2	2	6.0	72	1	1	2.5	100	10	10	10.0
17	1	1	1.8	*45	3	10	10.0	73	1	1	2.3	101	0	0	1.4
18	1	1	2.0	46	3	3	5.0	74	4	4	7.5	102	2	2	2.3
19	1	1	3.0	47	3	3	6.0	75	0	0	3.0	103	1	1	4.2
20	2	2	6.0	48	4	4	7.5	76	10	10	10.0	104	10	10	10.0
21	1	1	3.0	*49	0	1	3.7	77	2	2	10.0	105	1	1	4.2
22	0	0	1.8	50	0	0	4.2	78	0	0	3.7	106	0	0	1.4
23	10	10	10.0	51	1	1	6.0	79	1	1	2.5	107	0	0	3.7
24	2	2	7.5	52	5	5	7.5	80	10	10	10.0	108	0	0	1.4
25	1	1	5.0	53	7	7	7.5	81	10	10	10.0	109	0	0	7.5
26	2	2	6.0	54	5	5	6.0	82	1	1	5.0	110	4	4	7.5
27	2	2	3.0	*55	3	4	6.0	83	0	0	5.0	111	10	10	--
28	4	4	7.5	*56	10	4	7.5	84	0	0	2.7	112	4	4	7.5
												113	10	10	10.0
												114	10	10	--

Table 6. FINAL WEIGHTS ASSIGNED TO CHARACTERS BY SUCCESSIVE APPROXIMATIONS AND IMPLICIT WEIGHTING IN THE TWO ANALYSES OF SERIES II, PART 1. The column labeled **Char** shows the number of each character as in Table 2. Columns labeled **226** and **336** refer to the islands with those numbers of trees, as explained in the text; the column labeled **IW** shows the weights assigned by implicit weighting as implemented by the program PeeWee. Characters marked with an asterisk received different weights in the successive weighting based on the two islands of trees. A "--" in a column means that the character is uninformative in that data matrix.

as the basal clade, followed successively by Halictidae, Andrenidae + Oxaeidae, *Ctenocolletes,* and Colletidae (including Euryglossinae). The arrangement of genera within family groups in these analyses varies strikingly within Colletidae, but not in other S-T bees. Successive weighting based on the I-226 trees yields a tree (Fig. 13) in which Diphaglossinae (node I) are the basal clade within Colletidae, and *Mourecotelles* + *Colletes* are the sister group of a clade (node P) consisting of Xeromelissinae *(Chilicola),* Euryglossinae (node B), and Hylaeinae (node J). Successive weighting based on the I-336 trees (and the smaller island of 84 trees found by PAUP) yields a tree (Fig. 14) in which Diphaglossinae (node I) are a terminal lineage within Colletidae, sister group to *Colletes* + *Mourecotelles.*

Implied Weighting. This weighting procedure found a single fittest tree, with fit = 623.8 (Fig. 15). As in all other Series II trees except those of island-226 from the analyses with equal weighting, this tree shows the MCL-T bees as the basal clade of bees, followed sequentially by Halictidae, Andrenidae, Stenotritidae, and Colletidae (including Euryglossinae).

Relationships within the MCL-T clade and Halictidae are exactly the same as in the Series I analyses using implied weights (cf. Fig. 6). Within the Andrenidae, *Andrena* + (*Euherbstia* + *Alocandrena*) is a clade that is a sister group of *Protoxaea* and the remaining andrenids. Relationships within the latter clade are exactly as in the Series I analyses. Within the Colletidae, only *Callomelitta* and *Mydrosoma* occupy slightly different positions in the implied weights analyses from Series I and Series II.

SERIES II, PART 2: ANALYSES BASED ON FAMILY GROUNDPLANS

Two family groundplans were reconstructed, to reflect the range of phylogenetic hypotheses resulting

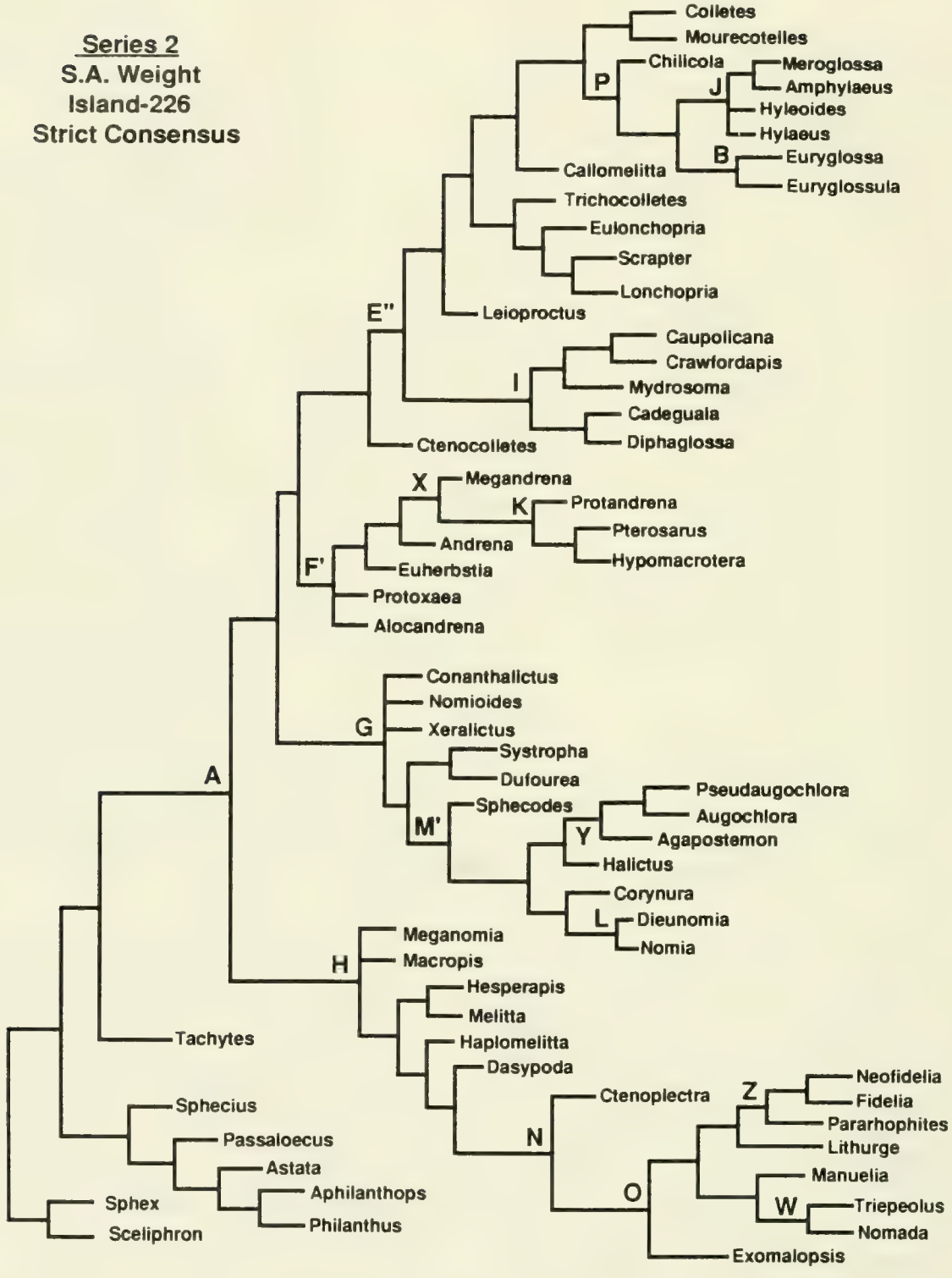


Fig. 13. Strict consensus tree for 14 trees found in the Series II analysis using exemplars and successive approximations weighting applied to island-226.

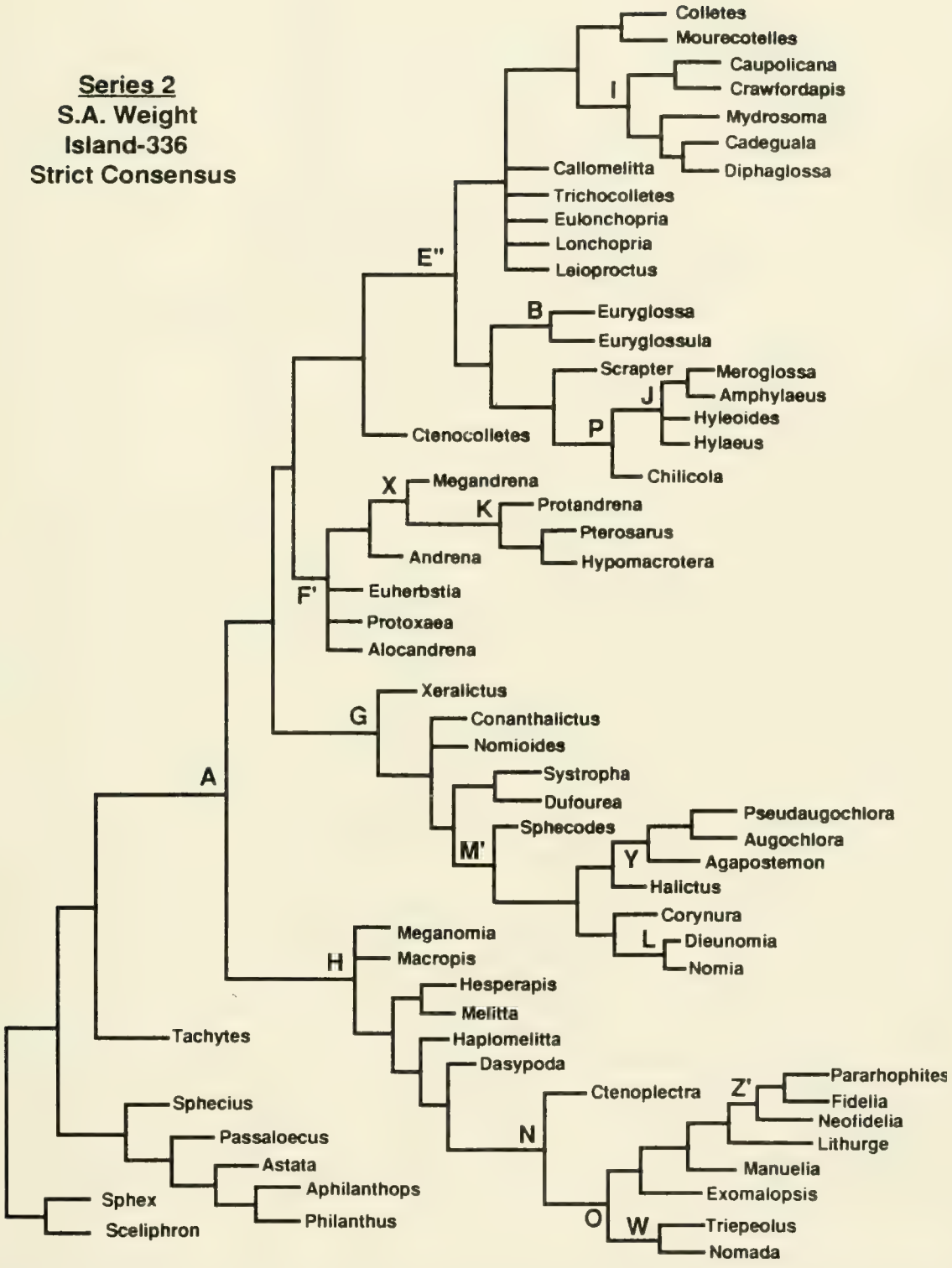


Fig. 14. Strict consensus tree for 206 trees found in the Series II analysis using exemplars and successive approximations weighting applied to the island of 336 trees from the NONA analysis.

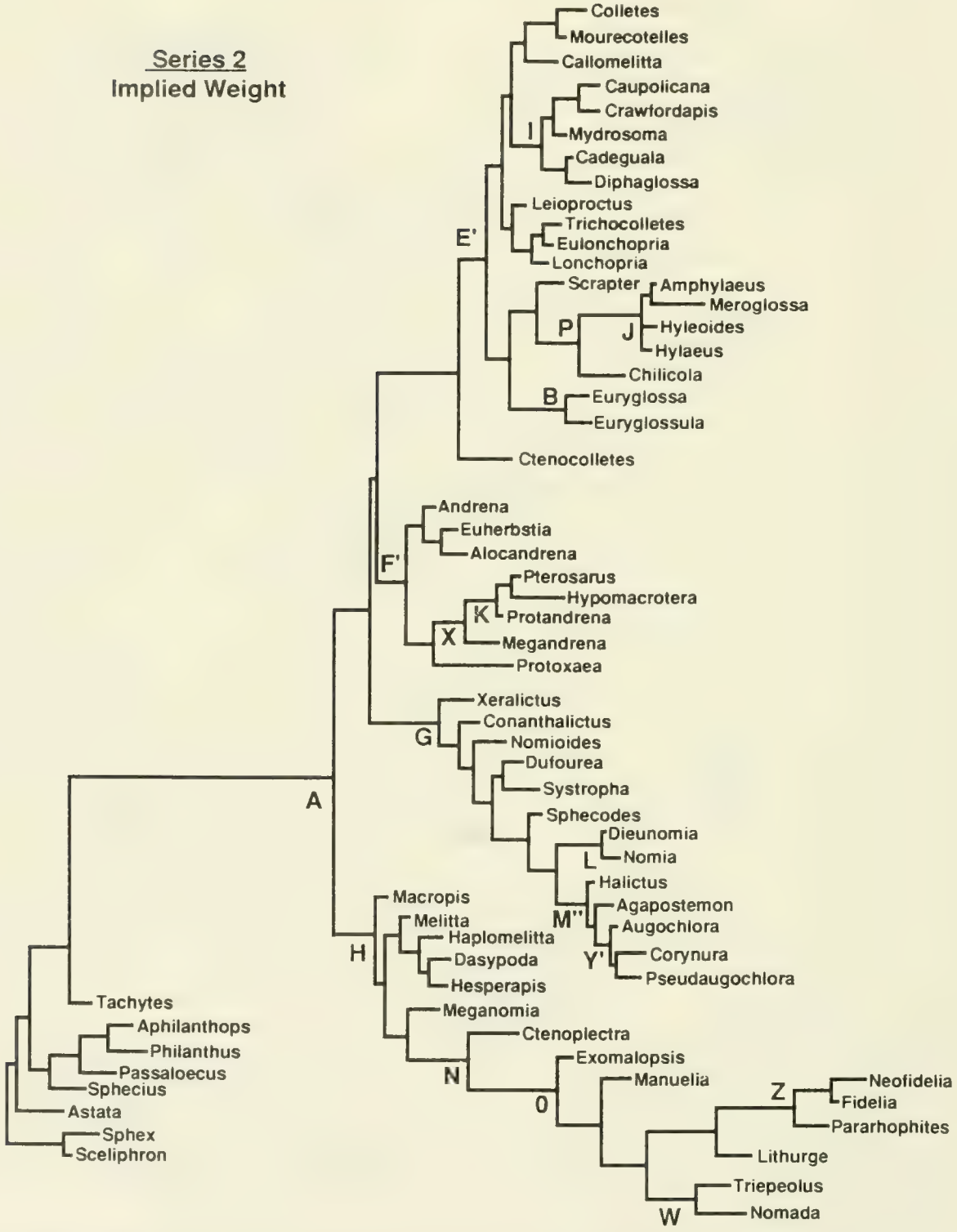


Fig. 15. Single fittest tree found in the Series II analysis using exemplars and implied weights.

Char	226	336	Char	226	336
2	10	10	**57**	2	2
3	10	10	**58**	2	2
4	10	10	**61**	10	10
7	10	10	**63**	10	10
8	0	10	**64**	10	10
12	10	--	**65**	2	10
17	2	--	**66**	2	--
19	0	3	**71**	--	10
22	3	10	**72**	--	10
27	10	--	**75**	--	2
37	4	10	**79**	10	10
38	3	0	**85**	10	10
39	--	0	**87**	--	10
40	0	0	**92**	0	10
41	0	0	**101**	10	10
42	0	--	**102**	10	3
53	10	10	**106**	10	3
54	10	10	**108**	10	--

Table 7. FINAL WEIGHTS ASSIGNED TO INFORMATIVE CHARACTERS BY SUCCESSIVE APPROXIMATIONS IN THE TWO ANALYSES IN SERIES II, PART 2. The column labeled **Char** gives the number of each character as in Table 2. Columns labeled **226** and **336** refer to analyses based on family groundplans with those designations (see text and Table 4 for details). A "--" in a column means that the character is uninformative in that data matrix.

from the exemplar-based analyses described above. The same terminal taxa are used in these analyses as in the groundplan analyses from Series I, even though Euryglossinae were consistently grouped with other colletids in all Series II analyses using exemplars. In the following discussion, *I-226 groundplans* will refer to family groundplans based on the strict consensus tree for the island of 226 trees found when all characters were given equal weight (Fig. 10). *I-336 groundplans* will refer to family groundplans based on the strict consensus tree for the island of 336 trees found when all characters were given equal weight (Fig. 12). All searches were exact, using PAUP's branch-and-bound algorithm.

I-226 Groundplan. This analysis was based upon 31 informative characters (Table 7). With all characters given equal weight, there was one most parsimonious tree (Fig. 16), with L = 92, ci = 0.84, ri = 0.67. This tree was stable to successive approximations and implied weighting. The only difference in the arrangement of families on this tree and its precursor (Fig. 10) is the placement of *Ctenocolletes.* Rather than being embedded within the Colletidae, it is the sister group of *Protoxaea,* and these two genera are the sister group of Andrenidae. A sister group relationship between *Ctenocolletes* and *Protoxaea* was hypothesized in the exemplar-based analyses in Series I that gave equal weight to all characters (Fig. 5), and in the EQWT groundplan analysis in Series I.

I-336 Groundplan. This analysis was based upon 30 informative characters (Table 7). With all characters given equal weight, there was one most parsimonious tree (Fig. 17), with L = 85, ci = 0.87, ri = 0.68, stable to successive approximations and implied weighting. As with the I-226 groundplans analysis, the I-336 groundplan differs from its precursor (Fig. 14) only in the placement of *Ctenocolletes,* which is again hypothesized to be the sister group of *Protoxaea.*

DISCUSSION

1. *General.* The major focus of this study is six groups of S-T bees that have often been treated as families: Andrenidae, Colletidae, Halictidae, Melittidae, Oxaeidae, and Stenotritidae. Our aim has been to include enough exemplars to establish whether the larger families (the first four listed above) are monophyletic, how they are related to one another and to L-T bees, and where the smaller families (the last two listed above) fit among the bees as a whole. Some understanding of phylogenetic structure within the larger families of S-T bees has also been achieved, but too few genera have been included to justify firm conclusions about relationships within these families. In some cases our results are fully consistent with the existing subfamilial and tribal classifications; in other cases they are not. More detailed studies of each family will be necessary to evaluate the significance of the groupings we have found.

Even with the use of exemplars, the number of taxa that must be used in a study of this scope is so large that approximate searches for the shortest trees are unavoidable. Our results have reaffirmed what specialists in parsimony methods (e.g., Maddison, 1991; Swofford and Begle, 1993) have emphasized: when doing approximate searches, explore several options.

By using the results of our analyses based upon exemplars to reconstruct family groundplans, we were able to produce a matrix with far fewer taxa, so that exact rather than approximate searches could be done. The results of these searches were also more decisive than in the exemplar analyses. In two of the four groundplan analyses, a single most parsimonious tree was found, and in all analyses the results were stable to successive and implied weighting.

However, the reason we performed four groundplan analyses rather than one was because of uncertainty about the best hypothesis for the groundplan of each family. Although there is much similarity in the groundplans derived from different initial trees, the differences that exist lead to different hypotheses about the relationships among families of S-T bees.

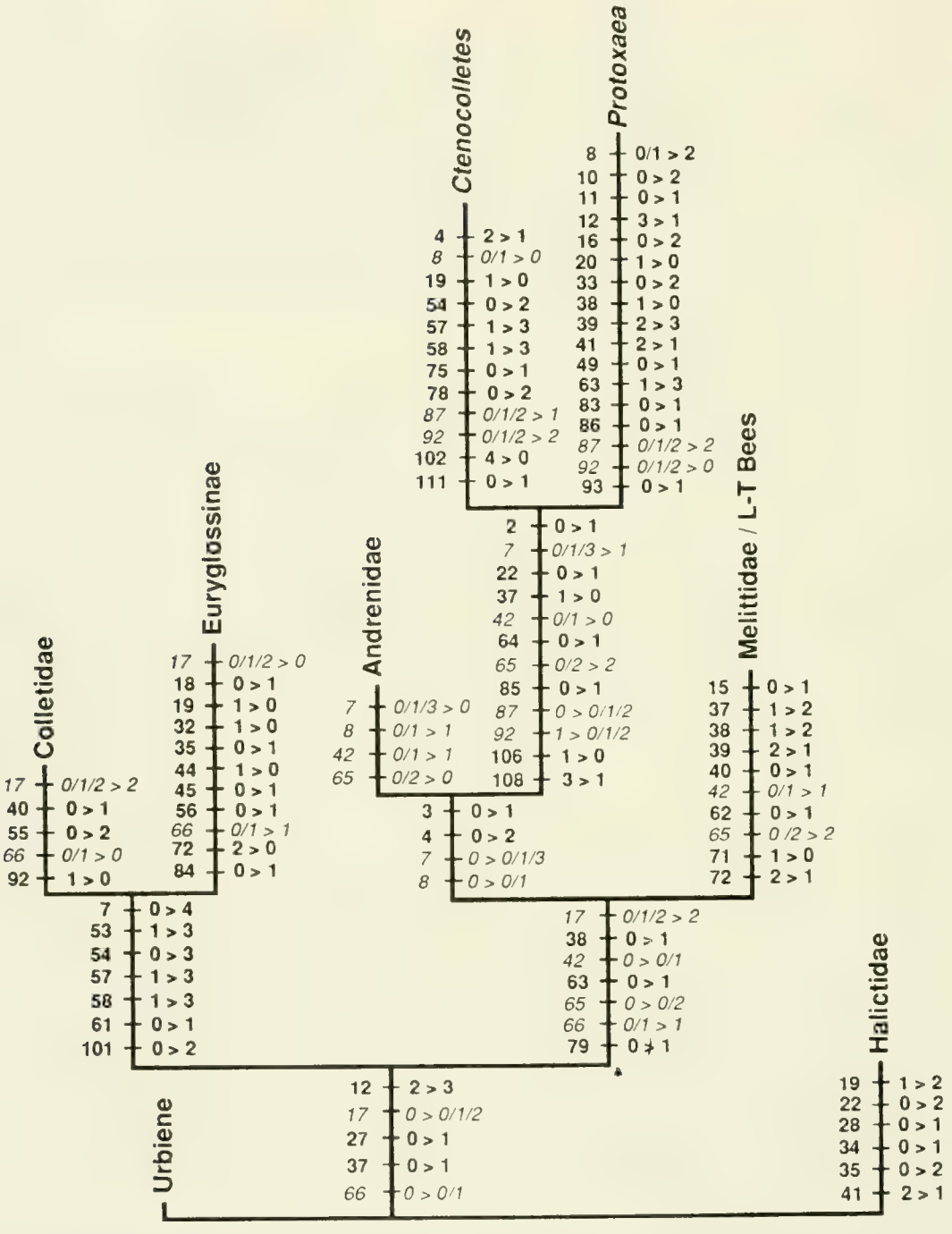


Fig. 16. The single most parsimonious tree found in the Series II analysis using island-226 groundplans. The same tree was found with equal, implicit, or successive approximations weighting.

Furthermore, the characters that provided the additional resolution that was achieved in the groundplan analyses vary at least as much within families as between them. It is only because groundplan analyses ignore this variation that they achieve greater resolution. The characters are subject to so much variation within families that the state that characterizes the groundplan of a family may mean little. The wisdom of basing phylogenetic hypotheses upon such highly variable characters is dubious.

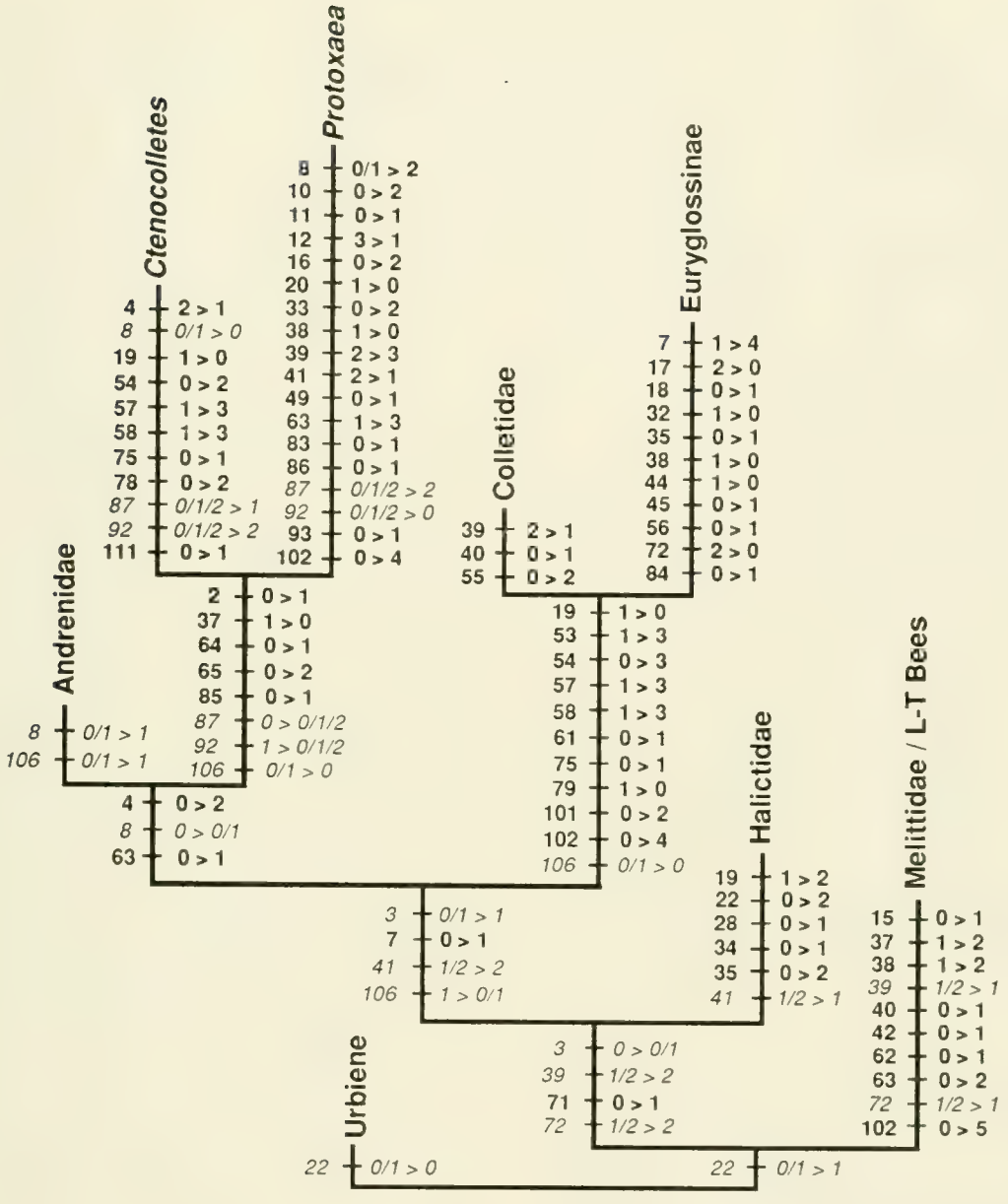


Fig. 17. The single most parsimonious tree found in the Series II analysis using island-336 groundplans. The same tree was found with equal, implicit, or successive approximations weighting.

Nevertheless, some general conclusions about the phylogeny of S-T bees can be drawn from our studies. We will discuss each of the families in turn.

2. *Colletidae.* This has long been regarded as the basal, or "most primitive," lineage of bees (e.g., Michener, 1944, 1979), and its diagnostic characters have been widely regarded as plesiomorphies for bees. Consequently, in the analyses of Series I, in which character codings reflect this traditional interpretation of the colletid glossa (as well as other characters), it might be expected that a cladistic analysis would show Colletidae to be a paraphyletic basal group. This is indeed the case in the exemplar analysis with equal weighting for all characters. The twenty exemplars of Colletidae s.l. are a basal paraphyletic group within the bees because the two euryglossine genera (Fig. 5, node B) are not included in the clade containing the other eighteen colletids (Fig. 5, node E). However, when implied weighting is used (recall that we cannot do successive approximations weight-

ing with the set of 4,296 equally parsimonious trees found with equal weighting in Series I), the four fittest trees show the twenty genera of colletids to form a single clade (Fig. 6, node E') that is the sister group to all bees except *Ctenocolletes*.

The results of the groundplan analyses in Series I exactly parallel those of the exemplar analyses: Euryglossinae are the basal clade of bees in the EQWT groundplan (Figs. 7, 8), whereas *Ctenocolletes* is the basal clade of bees and Euryglossinae are the sister group of the rest of the Colletidae in the IW groundplan (Fig. 9).

The idea that the strictly Australian taxon Euryglossinae is the sister group to all other bees, as suggested by Figures 5, 7, and 8, is attractive and could be correct. However, when characters are differentially weighted according to how much homoplasy they exhibit, the Euryglossinae are consistently placed within a monophyletic Colletidae. One of the more striking characters supporting this placement is the hypertrophied galeal comb and crescentic sclerite supporting it (state 27-2, Fig. 4), probably associated with carrying pollen to the nest in the crop instead of externally. This structure is found only in Euryglossinae and Hylaeinae. (It is smaller, presumably reduced, in the minute *Euryglossula,* for which it is coded as 27-1.) The Hylaeinae are not basal among colletids in any of our analyses (incidentally indicating that lack of the scopa in this lineage is a derived rather than an ancestral character). The relationship of Euryglossinae, Hylaeinae (and Xeromelissinae) and the nonbasal position of these groups in the Colletidae is further supported in McGinley's (1981) analysis of larval characters, although in one analysis Euryglossinae is associated with a *Colletes-Scrapter* clade.

In the analyses of Series II, which *a priori* interpret certain features of the colletid glossa as apomorphic, the twenty genera of Colletidae including Euryglossinae in the exemplar analysis consistently form a monophyletic group, regardless of whether we use equal, successive, or implied weighting (Figs. 10-15). [However, *Ctenocolletes* is deeply imbedded within Colletidae s. l. in the phylogenies based on one island of trees found with equal character weighting (Fig. 10). In the other analyses in Series II, *Ctenocolletes* is the sister group of Colletidae, including Euryglossinae.]

In the Series II groundplan analyses, Colletidae + Euryglossinae consistently form a monophyletic group, but *Ctenocolletes* is not the sister group of this clade.

In both Series I and Series II, two features of the colletid (including euryglossine) glossa are consistently interpreted as synapomorphies in every analysis we performed:

54-3. Blunt annular hairs of the glossa. State 3 occurs in all colletids except *Colletes,* which has state 54-2 (the latter state also occurs in *Ctenocolletes).*

61-1 Apical glossal lobes derived from the disannulate surface and bearing a glossal brush. Only colletids have this character state (the absence of this structure in males of *Meroglossa* is interpreted as a secondary loss and coded as a derived state, 61-2).

In Series I, the truncate or bilobed glossa (53-0) of most colletids (modified in Diphaglossinae, node I in Fig. 5) was inferred to be plesiomorphic for bees. In Series II, this same glossal shape was coded as a derived character for colletids (53-3) and was consistently interpreted as a synapomorphy for Colletidae (including Euryglossinae).

One other character was consistently interpreted as a colletid synapomorphy in all analyses in which Colletidae (including Euryglossinae) was monophyletic:

101-2 Absence of a pygidial plate in males. All colletids in our study share this character state, but so do *Aphilanthops* and *Passaloecus* among the spheciform wasps, as well as three andrenids, six halictids, four melittids, *Ctenoplectra,* and two L-T bees. This character would have a low consistency index on any parsimonious tree using our 65 exemplars, and its groundplan state for Colletidae is equivocal in many analyses.

McGinley's (1981) cladistic analysis of colletid larval characters resulted in phylogenies quite different from ours, based on adult characters. Diphaglossinae was the basal branch in all his trees. A finding of great interest is that *Colletes* was the sister group of *Scrapter* (or of *Scrapter* + *Euryglossa*) and that these were in a different clade from the other Colletinae.

3. *Stenotritidae.* The only two genera of this family are similar except in male genital and sternal characters. For this reason we used only one exemplar *(Ctenocolletes).* Since we excluded obvious autapomorphies in our initial selection of characters, the monophyly of Stenotritidae was not tested in our study. However, its phylogenetic position with respect to other lineages of S-T bees was analyzed, and the results are of interest, both because they were so inconsistent and because they have an important bearing on conclusions about the monophyly of Colletidae in the Series I exemplar analyses. No other taxon in our study showed such a radical shift in position in analyses with equal weighting vs. differential weighting based on levels of homoplasy shown by individual characters. In every analysis, many characters were hypothesized to change state in the *Ctenocolletes* line. This indicates that this taxon has a large number of unique states and/or derived states shared with a large and heterogeneous assemblage of other bees. If one compares the hypothesized autapomorphies for Stenotritidae across all the analyses we performed, there are only two that show up in every analysis:

4-1. Inner subantennal suture present, meeting or closely approaching outer subantennal suture at upper margin of clypeus. Among the taxa in our study, this state is unique to *Ctenocolletes.* The Andrenidae and *Protoxaea* have state 2 for this character, and this is one reason why *Ctenocolletes* is placed in the andrenid/oxaeid clade in several analyses (although character 4 was treated as nonadditive in all our analyses).

54-2. Annular hairs of glossa short, blunt or capitate. *Colletes* is the only other genus in our study with this character state. The other colletid genera, including

euryglossines, have state 3; whereas state 0 characterizes spheciform wasps and most other bees, except for certain halictids which have their own unique state (coded as 1).

Our analyses presented four distinctly different hypotheses about the phylogenetic position of Stenotritidae:

a. It is the sister group of Oxaeidae (the result based on equal weighting of all characters in Series I and the groundplan analyses, except for one of the two trees found with equal weighting in the IW groundplan analysis in Series I).

b. It is the sister group of all other bees (the result found with implied weighting in the exemplar analysis in Series I, and one of the solutions in the Series I EQWT groundplan analysis).

c. It is the sister group of Colletidae, including Euryglossinae (the result found in all but one of the exemplar analyses in Series II).

d. It is the sister group of the six colletid genera subtended by node I' on Figure 10 (island-226 in the Series II analysis with equal weighting for all characters). Five of the six genera at node I' are in the new world subfamily Diphaglossinae; *Trichocolletes* is an Australian genus in the subfamily Colletinae.

McGinley's (1981) larval study resulted in a fifth placement, Stenotritidae being the sister group of Colletinae other than *Colletes*. It should be noted, however, that McGinley's study assumed stenotritids to be a group within the Colletidae.

Each of our hypotheses involves a relatively long list of putative adult synapomorphies supporting the placement of *Ctenocolletes,* but in each case the overall pattern of distribution of these characters shows them to be highly labile and/or of uncertain polarity. The true phylogenetic position of the Stenotritidae is not clearly established by our study. The current geographic distribution of the group (strictly Australian) is most easily explained if it is more closely related to basal, Australian lineages of colletids than to the new world oxaeids or Diphaglossinae.

4. *Andrenidae (and Oxaeidae).* Our analyses consistently indicate that Andrenidae as they have traditionally been understood are paraphyletic with respect to Oxaeidae. Rozen's (1993, 1994) studies of larvae show the same result; his analyses consistently show *Euherbstia* and Oxaeidae as sister groups. Only one character state in our data matrix is consistently postulated to be a synapomorphy for Andrenidae + Oxaeidae in every analysis. Our analyses have found no synapomorphies consistently shared by Andrenidae but not Oxaeidae. The one consistent synapomorphy for these two groups is:

4-2. Inner subantennal suture present and widely separated from outer subantennal suture. This character state is unique to the Andrenidae/Oxaeidae and is present in all exemplars of this clade in our study. (Males of some Panurginae have only one subantennal suture, but this may be a secondary loss.)

Michener (1944) suggested that the possession of two subantennal sutures was evidence of a close phylogenetic relationship between oxaeids and andrenids, and treated Oxaeinae as a subfamily within Andrenidae. Rozen (1964) questioned this on the basis of striking differences between the larvae of the two groups, although he also stated that the distinctive features of the larva of *Protoxaea gloriosa* appeared to be unique to it (and thus probably autapomorphic). The many differences between oxaeid and andrenid larvae do not mean that the former could not be derived from the latter; see Rozen (1993, 1994).

Oxaeidae contain two to four genera, according to one's inclination to split. Because they are all morphologically uniform with respect to nearly all the characters used in this study, it is unlikely that adding more exemplars to our matrix would have altered the results of our analyses.

5. *Halictidae.* This is the only S-T bee family represented by more than one exemplar that is consistently and unequivocally shown as monophyletic in all of our analyses. Five character states are consistently hypothesized to be synapomorphies for this clade.

19-2. Wall of proboscidial fossa fused to tentorium forward almost to the clypeus. This character state is unique to Halictidae, and present in all halictid exemplars in our study.

22-2. Cardo attached to articulatory process of head just behind clypeus. This state is present in every halictid in our study, but it also occurs in *Chilicola* and *Scrapter* in the Colletidae and *Pterosarus* in the Andrenidae.

28-1. Base of galea tapering gradually to a point overlapping at least half length of stipes. This character state is present in every halictid in our study, but also occurs in *Chilicola* (Colletidae).

34-1. Lacinia stretched up anterior surface of labiomaxillary tube. This character state is unique to Halictidae, and present in all of our exemplars.

35-2. Lacinia finger-shaped. This state is also unique to Halictidae and present in all our exemplars of the family. Other states of this character have a less orderly distribution among taxa (see Table 2).

Although the monophyly of Halictidae as a family is well supported by our study, relationships within the family are among the least stable components of our various analyses. The frequent failure of the three genera now placed in Augochlorini (*Augochlora, Pseudaugochlora,* and *Corynura*) to show up as a monophyletic group is particularly puzzling, because one of the most distinctive diagnostic features of this tribe, the apicomedian cleft on T5 (state 97-2), would appear to be an obvious synapomorphy. Likewise the lack of a pygidial plate in the male (state 101-2) differentiates these genera from other Halictinae. These characters are given enough weight by the implied weighting procedure that Augochlorini are supported as a monophyletic group (Figs. 6, 15, node Y') in all analyses that used this type of weighting, but with

equal or successive weighting the Augochlorini do not form a monophyletic group. The widely different placements of Nomiinae (*Dieunomia + Nomia*) in different analyses are also problematic. These matters require further study using a larger sample of taxa.

6. *Melittidae + L-T Bees.* Our six exemplars of Melittidae as it is usually understood, *Dasypoda, Haplomelitta, Hesperapis, Macropis, Meganomia,* and *Melitta,* consistently formed a paraphyletic grouping at the base of a clade that also contained *Ctenoplectra* (supposed by R-AM to be a derivative of L-T bees) and the L-T bees. This was not a surprising result; this pattern of relationships was proposed by Michener and Greenberg (1980). The following six character states were consistently hypothesized to be synapomorphies shared by some members of the MCL-T clade.

15-1 Shallow postoccipital pouch below foramen magnum. All other S-T bees and spheciform wasps in our analysis have state 0, as do all L-T bees except *Exomalopsis* and *Triepeolus.* None of our melittids have state 0, but four of them have state 2 (a distinct and deep pouch), as does *Ctenoplectra.*

37-2. Lorum V-shaped with slender arms. State 2 occurs in all members of the MCL-T clade, and elsewhere among our exemplars only in *Lonchopria* (Colletidae), in which the V-shaped condition is only moderately developed. States 0 and 1 are distributed more erratically among S-T bees (Table 2).

38-2. Apex of lorum and base of mentum together projecting posteriorly as a long lobe from labiomaxillary tube. State 2 occurs only in the MCL-T clade and is present in all its members; states 0 and 1 are distributed among other S-T bees (Table 2).

40-1. Base of mentum curled to attach to or abut against lorum. State 1 occurs in all members of MCL-T clade except *Lithurge;* it also occurs in four colletids and three andrenids (Table 2).

62-1. Apophyseal arms of prosternum separate from one another. All bees outside the MCL-T clade have state 0, although state 1 occurs in three of our spheciform wasp exemplars; parsimony clearly indicates a separate derivation of state 1 in the MCL-T clade and in the wasps. Within this clade, state 1 occurs in all melittids and *Ctenoplectra,* but all true L-T bees except *Manuelia* have state 0.

65-2. Profile of metanotum slanting. Although all our spheciform wasp exemplars have state 0, this character has a very erratic distribution among bees. State 2 occurs in *Ctenocolletes,* seven colletids, one halictid, five melittids, and five L-T bees (see Table 2).

The most recent review and classification of Melittidae (Michener, 1981a) recognizes three subfamilies and nineteen genera, three of which are further divided into subgenera. Our sample of six melittid exemplars is sufficient to establish the paraphyly of the family as presently defined. See comments on bee classification below for further discussion of phylogenetic relationships within this paraphyletic assemblage. It may or may not be significant that the two melittid subfamilies represented by more than one exemplar in our studies, Dasypodinae *(Dasypoda, Haplomelitta, Hesperapis)* and Melittinae *(Melitta, Macropis),* are not consistently shown to be monophyletic. [With implied weighting, Dasypodinae are monophyletic (Figs. 6, 15), but Melittinae never are.] Michener's (1981a, figs. 1, 2) cladograms show several synapomorphies for Dasypodinae and Meganomiinae, but one or none for Melittinae and none for the family as a whole. Roig-Alsina and Michener (1993) found a minute triangular sclerite in the cardo-stipital articulation only in the Melittidae, although absent (lost?) in *Hesperapis.* We found this sclerite not only hard to find but absent in some preparations, and did not include it in our study. If it were consistently present, it could be a synapomorphy of Melittidae.

The monophyly of L-T bees, including Ctenoplectridae, is thoroughly discussed in Roig-Alsina and Michener (1993). The only noteworthy thing about this clade in our study is that *Ctenoplectra* was consistently placed as the basal lineage of L-T bees, as in Michener and Greenberg's (1980) study. In Roig-Alsina and Michener's study, as well as an ancillary study by Silveira (1993), *Ctenoplectra* was deeply embedded within the L-T bees, appearing near the Eucerini, Tapinotaspini, etc. Our studies included no exemplars of these tribes. It is therefore not surprising that its relation to L-T bee taxa is not revealed in our study.

7. *Relationships Among S-T Bee Families.* The various analyses presented above lead to widely varying conclusions about phylogenetic relationships among the families of S-T bees. A strict consensus tree for the results from all the analyses would be a completely unresolved polytomy of the family-level groups. On the other hand, the number of possible cladograms for seven taxa (this is the number of ingroup taxa used in the family groundplan analyses) is far greater than the number of cladograms that were found to be most parsimonious in our analyses, so it would be erroneous to conclude that this study does not support any conclusions at all about the relationships among families of S-T bees. It just has not provided unequivocal support for a single phylogenetic hypothesis, even though there cannot be more than one phylogenetic history for these taxa.

The analyses in Series I use conventional methods of outgroup comparison to polarize characters. These analyses consistently find the colletid genera to belong to a relatively old lineage in Apiformes. When all characters are given equal weight, these genera form a paraphyletic basal assemblage (Figs. 5, 7, 8). When implied weighting is used, colletids are a monophyletic sister group of all other bees except Stenotritidae (Figs. 6, 9).

In the Series I analyses, three characters associated with a pointed glossa (53-1, glossa shape; 57-1, disannulate surface of glossa; 58-2, serriate hairs of glossa) are interpreted as the principal synapomorphies shared by all bees except colletids and stenotritids. One additional character (19-1, wall of

proboscidial fossa fused to tentorium forward to middle of head) is also consistently hypothesized to be a synapomorphy for this clade. However, this appears to be a very labile character, and thus not very reliable in a phylogenetic analysis. The state found in spheciform wasps, stenotritids, and many colletids (19-0) also occurs in all three panurgines, *Neofidelia,* and *Pararhophites,* whereas state 19-1 occurs in seven of our colletid genera. Halictids have their own unique state for this character.

Thus, the three characters (53, 57, and 58) that are split up and coded differently in the analyses of Series I and II are of major importance in resolving relationships among groups of families. The analyses in Series II postulate a transformation series in which these three characters, whose states in spheciform wasps and colletids look similar, are nevertheless coded as nonhomologous. When all characters are given equal weight, there are two islands of equally parsimonious trees with substantially different topologies (Figs. 10, 11). Trees of neither island show colletids or stenotritids as the basal lineage of bees, although those of island-226 have colletids as the sister group of all bees except halictids (Fig. 10). With successive approximations or implied weighting applied to either of these islands of trees, the most parsimonious trees had the MCL-T bees as the oldest lineage of bees, and colletids (including euryglossines) as one of the youngest clades in Apiformes (Figs. 13-15).

A principal reason for recoding three glossal characters in Series II was to evaluate the Perkins-McGinley hypothesis of glossal evolution. This hypothesis was proposed because of sexual dimorphism in the characters in certain genera of Australian hylaeine colletids, the males having the glossa similar to that of *Andrena* while the female has a typical hylaeine glossa. The character codings of Series II hypothesized that the sexual dimorphism was an intermediate state between an ancestral state in which both sexes had a pointed glossa and a derived state in which both sexes had a broadened truncate or bilobed glossa. If other characters were consistent with this transformation series, one might expect the sexually dimorphic colletid genera (exemplified by *Meroglossa* in our study) to occupy a basal position within Colletidae; however, none of our analyses produced such a result. *Meroglossa* is, in fact, not only in our study but in all previous classifications of Australian bees, consistently placed in the Hylaeinae, which are not a basal group of Colletidae in any of our analyses. When all characters are considered together, the pointed glossa and associated characters of *Meroglossa* males are interpreted in our analysis as reversals, although of course a parsimony analysis can provide no explanation of why such reversals would have occurred. Thus the Perkins-McGinley hypothesis of glossal evolution is not supported by our analyses.

These analyses do illustrate how a plausible hypothesis of evolutionary change in one set of characters may produce a very different hypothesis of phylogenetic relationships than an analysis based on a large number of characters. At the same time, the different tree topologies resulting from the analyses of Series I and II demonstrate that changes in the coding of only a handful of characters in a large data set can lead to very different results in a parsimony analysis. For these reasons, it seems best to regard the relationships among the major clades (families) of S-T bees as unresolved by this study.

It is interesting that a study such as ours failed to find clear resolution of the basal phylogeny of the bees. This is nothing new; throughout the history of efforts to provide a satisfying classification for bees, hymenopterists have produced diverse and unsatisfying results. Presumably these failures tell us something about the evolution of bees, but it is not clear what they tell us. The major clades (families) are distinct enough, but their relationships to one another remain uncertain; in one or another of our analyses every major clade except Andrenidae appears as the sister group to all other bees. Possibly the bees have suffered fewer extinctions of basal branches than groups in which relationships among major clades are clear, but this is hardly an explanation of our results. The problems within families can probably be partly resolved by use of more taxa, more closely related outgroups, and possibly additional adult characters, but we believe that the problems in determining relationships among families are unlikely to be resolved by such means. New sets of characters (e.g., larval, molecular) should be tried.

8. *Biogeography and Fossil Bees.* The basal lineages in bee phylogeny bring up some interesting biogeographical and paleontological considerations. In some analyses, the Stenotritidae *(Ctenocolletes)* are the sister group to all other bees. The distribution of this family, which has two small genera both limited to Australia, is in accordance with a basal position because Australia is the home of various archaic animals.

In other analyses the Halictidae are the basal group. Halictids are abundant worldwide and biogeography contributes nothing to this alternative phylogenetic hypothesis.

In some analyses, Colletidae, with or without the Euryglossinae, are the basal group. Euryglossines are found only in Australia. The Hylaeinae are richly developed and diverse in Australia, while other continents have principally one widespread genus, *Hylaeus.* The Xeromelissinae and Diphaglossinae are diverse in South America, with outliers as far north as

Mesoamerica for Xeromelissinae and North America for Diphaglossinae. The Colletinae are richly developed and diverse in Australia and temperate South America, with one genus, *Leioproctus,* common to these two continents. Elsewhere, there is a genus *(Scrapter)* usually placed in Colletinae in southern Africa and there are a few outliers from South America in Mesoamerica, but only one widespread genus, *Colletes,* is in the holarctic region. [It should be noted that our study indicates that Colletinae is paraphyletic, and Michener (1989) found *Leioproctus* to be paraphyletic.] Thus the Colletidae have a largely disjunct southern distribution that, as for the Stenotritidae, suggests an archaic clade or clades.

Finally, analyses showing the MCL-T clade as the sister group to all other bees are less interesting from a biogeographical perspective, since L-T bees occur worldwide, but are of interest because of the fossil record. The oldest known bee is a late Cretaceous meliponine (Michener and Grimaldi, 1988; for comments on dating see Rasnitsyn and Michener, 1991). This is an L-T bee. More telling, the late Eocene Baltic amber contains a considerable number of bees. Of these there are 17 or more species of L-T bees, as listed by Zeuner and Manning (1976). There are, however, no colletids, no halictids, and three andrenids; two of the "andrenids" are nothing but reports in the last century of *Andrena,* made by persons who were not bee specialists, while only one is well enough preserved to have been described and to receive a specific name. It, however, is not an *Andrena* and probably is a "melittid." Whether any Baltic amber bees are actually andrenids is doubtful. There are eight species supposed to be in the Melittidae; their true familial relationships are not clear. Thus the known fossil record is consistent with an early origin of the MCL-T bees relative to other S-T bees. In further support of antiquity of MCL-T bees is the widely disjunct distribution of some melittids. *Hesperapis* and *Capicola* are almost the same genus, the former in western North America, the latter in southern Africa. Their closest relative is *Eremaphanta* from central Asia. These must represent an ancient clade if the phylogeny hypothesized by Michener (1981a) is correct. Moreover the pantropical distribution of the Meliponini, an L-T tribe, suggests antiquity since these bees show little vagility; for example, none or almost none reached the Antilles without human aid in spite of their abundance and diversity on the Caribbean continental margins.

A later sampling of bees, from the Oligocene of Florissant, Colorado, shows S-T and L-T bees more nearly equally abundant, with about 13 species of S-T plus one melittid and 16 L-T bees. Another sample of approximately the same age but more nearly comparable to the Baltic amber because the fossils are also in amber is from the Dominican Republic. It includes one meliponine (L-T) and the following S-T bees: three halictids, one colletid, and one andrenid (Michener and Poinar, in press). Again, unlike the Eocene, S-T families are well represented, as in the Recent fauna.

Fossil bees, especially those of the Eocene, are in serious need of reworking by a bee specialist. The counts mentioned above are subjective. Familial characters are often impossible to find in fossil bees, for many such characters are in the mouthparts, some in the base of the proboscis where they are difficult to see even in fresh specimens.

9. *Comments on Bee Classification.* The preceding parts of this paper present our phylogenetic results, based on the exemplars, the characters, and the character states that we used, in what we believe is an unbiased way. We were faced frequently with multiple equally parsimonious phylogenetic solutions. One of the attributes of taxonomic work, however, is that one must make decisions, commonly on the basis of conflicting or inadequate information, in order that the nomenclature and classification can serve their major functions: enabling users to know what others are talking about, i.e., information storage and retrieval. Lack of decisions does not result in usable classifications; decisions, even if arbitrary, should. An unfortunate effect of a classification is that the resultant taxa seem to acquire a reality that they do not necessarily deserve. To counter this tendency, we urge readers to remember that prior parts of this paper are often indecisive as to phylogenies, and also that building a classification on a phylogeny is a subjective process, certainly as to classificatory rank, but also as to philosophy, since people differ in their classificatory methods. There is no way to keep judgments out of the classificatory process, even if one knows the phylogeny with certainty. We can only claim that the classification presented below is based on more characters, more appropriately analyzed, than its antecedents, and that our methods have been more explicitly stated than in prior efforts with S-T bees. Because we made arbitrary decisions, others will sometimes reach different classificatory conclusions. We hope that, using other character sets, future researchers will reach more decisive phylogenetic conclusions. The biologically interesting and useful conclusions are phylogenetic; the classification also has practical significance for data storage and retrieval.

The following is an annotated account of the families of S-T bees.

A. FAMILY COLLETIDAE. In the Series II analyses and the Series I analyses with successive and implied weighting, the Colletidae is a monophyletic unit. We therefore choose to retain this family in the usual

sense. In the Series I analyses with equal weighting Colletidae are paraphyletic, with Euryglossinae appearing as a separate family-level unit.

1. Subfamily Colletinae. This diverse group is consistently paraphyletic. An analysis of many genera and subgenera, using other S-T bees as the outgroup, should be made.

2. Subfamily Diphaglossinae. This subfamily is monophyletic in every analysis except in one in Series II (Fig. 10). It could be united with the Colletinae, although the latter would still be paraphyletic. Larvae of Diphaglossinae spin strong cocoons and have the cephalic structures of cocoon-spinning bees (Rozen, 1984), while larvae of all other Colletidae spin no cocoons and have reduced tactile and spinning structures. Thus all other Colletidae have synapomorphic character states relative to Diphaglossinae. McGinley's (1981) cladograms based on larvae show Diphaglossinae as the sister group to other colletids. For these reasons it would be premature to accept the indication of our analyses that Diphaglossinae are derived Colletinae. The tribes of Diphaglossinae recognized by Michener (1986) are also consistently shown to be monophyletic, although the number of exemplars is minimal.

3. Subfamily Hylaeinae. This monophyletic unit is the sister group to the Xeromelissinae (*Chilicola* in our study) except that in Figure 13 it is the sister group to Euryglossinae, the two together being the sister group to Xeromelissinae.

4. Subfamily Xeromelissinae (*Chilicola* in our study). See above.

5. Subfamily Euryglossinae. In analyses in Series I this monophyletic subfamily appears as the sister group to all bees, to all other colletids, or to Hylaeinae. In analyses in Series II it appears as the sister group to all other colletids or is embedded in the Colletidae.

B. FAMILY STENOTRITIDAE. *Ctenocolletes,* the exemplar of this family in our study, appears in such diverse positions in our various figures that its true phylogenetic position is uncertain. Since it can only occupy one position in a classification, we consider it to be a distinct family.

C. FAMILY ANDRENIDAE. This family is consistently monophyletic if *Protoxaea* (commonly placed in the family Oxaeidae) is included.

1. Subfamily Andreninae. This group as currently understood is consistently paraphyletic, giving rise to both Panurginae and Oxaeinae. It should be reanalyzed, with more genera and subgenera, and with other S-T bees as outgroups.

2. Subfamily Panurginae. This is a consistently monophyletic unit.

3. Subfamily Oxaeinae. Because of numerous autapomorphies, this group has often been accorded familial rank, although it was placed in Andrenidae by Michener (1944). Our analyses indicate that it is an andrenid lineage with numerous autapomorphies. After a study of larvae, Rozen (1993, 1994) also considered Oxaeinae as derived from a paraphyletic Andreninae and sister group to *Euherbstia.*

D. FAMILY HALICTIDAE. This family is consistently monophyletic. The relationships among included taxa shown by our analyses are diverse. The family badly needs reanalysis with more taxa, and with other S-T bees as outgroups.

1. Subfamily Rophitinae. This group appears consistently paraphyletic, but in such different ways that an alternative classification is not now practical. Moreover, we may have neglected features that might constitute synapomorphies for the Rophitinae. The relatively small clypeus, large labrum, and low position of the antennae on the face are variable and difficult to quantify, yet give the rophitine face a distinctive aspect not shared by *Nomioides* or other bees. Results of our analyses should therefore be considered preliminary, and should not now influence the classification.

2. Subfamily Nomioidinae. *Nomioides,* our exemplar of this taxon, falls outside the Halictinae, where it is usually placed; in our analyses it is usually within the paraphyletic Rophitinae. Pesenko (1983) in a detailed study has also recognized the distinctiveness of the *Nomioides* group and considers it as the sister to Halictini + Augochlorini. He did not include Rophitinae in his study. All members of the Nomioidinae are similar, so that they are commonly placed in one genus; additional exemplars would add little to our knowledge of S-T bee diversity.

3. Subfamily Nomiinae. Although this subfamily is located in different places in the Halictidae in different analyses, its two exemplar genera are consistently sister groups. Thus the subfamily is monophyletic according to our analyses.

4. Subfamily Halictinae. When *Nomioides* is excluded from the Halictinae, this subfamily is monophyletic in some analyses, but in others the Nomiinae or some rophitines are intermixed with halictines. The halictine tribes, Halictini and Augochlorini, receive equivocal support at best. Halictini are consistently shown to be paraphyletic, and Augochlorini are only monophyletic in exemplar analyses that use implied weighting.

Sphecodes is a parasitic genus having various morphological characters associated with this way of life (Michener, 1978). It may be derived from the *Halictus* group of Halictini, yet in our analyses it is a basal branch of Halictinae (Figs. 5, 11) or is the sister group to the Nomiinae + Halictinae (Figs. 6, 13-15). If it is as old as these analyses suggest, the question arises as to its original host. Most species currently parasitize halictines in the *Halictus-Lasioglossum* complex,

although a wide range of other hosts, including andrenids and even L-T bees, are documented.

E. FAMILY MELITTIDAE. Our analyses all show that Melittidae in its ordinary sense (e.g., Michener, 1981a) is a paraphyletic group from which the L-T bees arose. We consider this relationship established. If one wishes to maintain L-T bee families (Megachilidae, Apidae), then according to cladistic principles the Melittidae would have to be broken into three or more families. Alternatively, the melittid genera could be put in a single family that would also include all the L-T bees; the rules of nomenclature dictate that such a family would be called Apidae. Of these two classificatory options, we favor partitioning Melittidae into three families. The principle weaknesses of this solution are that it multiplies an already relatively obscure family into three, and tends to conceal the relationship of these taxa to the L-T bees. However, this seems preferable to the confusion that would result from yet another redefinition of the widely used (and nomenclaturally unavoidable) name Apidae. CDM is not in principle opposed to paraphyletic taxa, providing the paraphyly is made clearly known, but the similarity of the melittoid families here recognized is not so great as to support retention of the status quo.

Only the analyses with implied weighting found a consistent pattern of relationships that could provide a basis for partitioning the paraphyletic Melittidae (sense of Michener, 1981a) into monophyletic families. The resolution of melittid relationships provided by implied weighting in our study is consistent with the results of a cladistic analysis of Melittidae done by Michener, which found two minimum-length trees (Michener, 1981a: figs. 1, 2) for a set of 102 morphological characters and 24 taxa representing genera and subgenera. The 1981 cladograms show only melittid genera and thus imply that Melittidae are monophyletic, although it was stated that no synapomorphies not shared with L-T bees could be found for the entire family. The principal taxa used for outgroup comparison were colletids and andrenids, and the trees were found with an early version of a parsimony program, obtained from James S. Farris, that used the Wagner algorithm (Farris, 1970).

Combining the results of our implied weighting analyses, which produced identical cladograms for the six melittid exemplars in Series I and Series II analyses, with Michener's study, one could partition the paraphyletic Melittidae as currently defined into four monophyletic families. Our sole exemplar of Melittidae s. str. is *Melitta;* other genera from Michener's 1981a revision would be *Dolichochile,* which is at best a subgenus of *Melitta,* and according to CDM, probably *Rediviva* and *Redivivoides.* These two genera could not be readily assigned to the redefined families by referring to Michener's 1981a cladograms. According to his Figure 1, *Rediviva* could be placed near *Macropis,* but there are no synapomorphies to link *Redivivoides* with either *Melitta* or *Macropis.* However, Michener's Figure 2, which he preferred in this respect, indicates that *Rediviva* and *Redivivoides* are sister taxa, themselves the sister group to *Melitta.* Further study is needed to confirm the phylogenetic position of these genera, and to reassess the placement of the other genera as well.

Finally, there is the genus *Macropis.* In our analyses, *Macropis* was frequently the basal branch of the melittoid group. However, as noted by Michener (1981a), *Macropis* shares a series of apomorphies with *Rediviva* (which was not included in our study). They are complex features unlikely to have arisen convergently, and are probably related to collecting and transport of floral oils. If they are synapomorphic for these two genera, possibly lost in others, these characters could indicate that *Macropis* should be included in the Melittidae. Rozen and McGinley's (1974) study of larvae provides a slight indication (one character in their "second most likely phylogeny") of a sister-group relation of *Macropis* to *Melitta;* the only sound conclusion is that their larvae are similar to one another and both are plesiomorphic in numerous characters relative to Dasypodidae, partly because they spin cocoons whereas those of Dasypodidae do not. In summary, we tentatively retain *Macropis* in the Melittidae, subject to further study.

F. FAMILY DASYPODIDAE. Our exemplars are *Dasypoda, Haplomelitta,* and *Hesperapis;* other genera would be *Promelitta, Samba, Eremaphanta, Capicola,* and *Xeralictoides.* (Michener's 1981a revision recognized a number of subgenera for several of these genera, and *Xeralictoides* is classified as a subgenus of *Hesperapis* in the recent treatment of North American bee genera by Michener et al., 1994.) Rozen and McGinley's (1974) study of larvae supported the phylogenetic relationship of *Capicola, Dasypoda,* and *Hesperapis.*

G. FAMILY MEGANOMIIDAE. Our exemplar is *Meganomia;* the other genera would be *Ceratomonia, Pseudophilanthus* and *Uromonia.* In a study of larvae, Rozen (1977) proposed that *Meganomia* is the sister group to all other Melittidae (sense of Michener, 1981a). Although in our study *Macropis* often occupies this position, *Meganomia* does so in Figures 11 and 12, where it is the sister group to other "Melittidae" plus L-T bees. The latter were not included in Rozen's analysis.

H. FAMILY MEGACHILIDAE. See Roig-Alsina and Michener (1993) for comments and subfamilial classification.

I. FAMILY APIDAE. See Roig-Alsina and Michener (1993) for comments and subfamilial classification. For comments on the Ctenoplectridae, see part 6 of the Discussion, above. Among the problems with recognizing Apidae in a new sense, i.e., as the MCL-T bees, are the numerous ways in which the word has been and is currently used. For some authors, Apidae is the family name for all bees. For some, it is the name for the L-T bees. For some, e.g., Roig-Alsina and Michener (1993), it is the name for all L-T bees except the Megachilidae. It can also be used for the Apinae of Roig-Alsina and Michener (1993). For many it is the name for the corbiculate bees. Finally there are those who use the name only for the genus *Apis*. Thus it is already not a very useful name; terms like L-T bees and MCL-T bees are more stable. We have decided not to modify the usage supported by Michener (1944) and Roig-Alsina and Michener (1993).

LITERATURE CITED

Alexander, B. A. 1992a. An exploratory analysis of cladistic relationships within the superfamily Apoidea, with special reference to sphecid wasps (Hymenoptera). Journal of Hymenoptera Research 1: 25-61.

Alexander, B. A. 1992b. A cladistic analysis of the subfamily Philanthinae (Hymenoptera: Sphecidae). Systematic Entomology 17: 91-108.

Bohart, R. M., and A. S. Menke. 1976. Sphecid Wasps of the World. Berkeley: University of California Press. ix + 695 pp.

Brothers, D. J. 1975. Phylogeny and classification of the aculeate Hymenoptera, with special reference to Mutillidae. University of Kansas Science Bulletin 50: 483-648.

Brothers, D. J., and J. M. Carpenter. 1993. Phylogeny of Aculeata: Chrysidoidea and Vespoidea (Hymenoptera). Journal of Hymenoptera Research 2: 227-304.

Eickwort, G. C. 1969. A comparative morphological study and generic revision of the augochlorine bees. University of Kansas Science Bulletin 48: 325-524.

Evans, H. E. 1959. Studies on the larvae of digger wasps. Part V: Conclusion. Transactions of the American Entomological Society 85: 137-191.

Farris, J. S. 1969. A successive approximations approach to character weighting. Systematic Zoology 18: 374-385.

Farris, J. S. 1970. Methods for computing Wagner trees. Systematic Zoology 19: 83-92.

Farris, J. S. 1972. Estimating phylogenetic trees from distance matrices. American Naturalist 106: 645-668.

Farris, J. S. 1988. Hennig86, Version 1.5. Port Jefferson Station, New York: distributed by the author.

Farris, J. S. 1989a. The retention index and homoplasy excess. Systematic Zoology 38: 406-407.

Farris, J. S. 1989b. The retention index and the rescaled consistency index. Cladistics 5: 417-419.

Finnamore, A. T. 1993. Series Spheciformes, pp. 280-386. *In* H. Goulet and J. T. Huber (eds.), Hymenoptera of the World: An Identification Guide to Families. Ottawa, Ontario: Research Branch, Agriculture Canada, Publication 1894/E.

Goloboff, P. A. 1993a. NONA—Version 1.1. New York, NY. Computer program distributed by the author.

Goloboff, P. A. 1993b. Estimating character weights during tree search. Cladistics 9: 83-91.

Goloboff, P. A. 1993c. Pee-Wee, Version 2.1. New York, NY. Computer program distributed by the author.

Jander, R. 1976. Grooming and pollen manipulation in bees (Apoidea): The nature and evolution of movements involving the foreleg. Physiological Entomology 1: 179-194.

Kluge, A. G., and J. S. Farris. 1969. Quantitative phyletics and the evolution of anurans. Systematic Zoology 18: 1-32.

Krombein, K. V. 1979. Superfamily Sphecoidea, pp. 1573-1740. *In* K. V. Krombein, P. D. Hurd, Jr., D. R. Smith, and B. D. Burks, Catalog of Hymenoptera in America North of Mexico. Washington, D. C.: Smithsonian Institution Press.

Lomholdt, O. 1982. On the origin of the bees (Hymenoptera: Apidae, Sphecidae). Entomologica Scandinavica 13: 185-190.

Maddison, D. R. 1991. The discovery and importance of multiple islands of most parsimonious trees. Systematic Zoology 40: 315-328.

Maddison, W. P., and D. R. Maddison. 1992. MacClade: Analysis of phylogeny and character evolution, Version 3.0. Sunderland, Massachusetts: Sinauer Associates.

McGinley, R. J. 1980. Glossal morphology of the Colletidae and recognition of the Stenotritidae at the family level. Journal of the Kansas Entomological Society 53: 539-552.

McGinley, R. J. 1981. Systematics of the Colletidae based on mature larvae with phenetic analysis of apoid larvae. University of California Publications in Entomology 91: i-xvi + 1-307.

Meacham, C. A. 1984. The role of hypothesized direction of characters in the estimation of evolutionary history. Taxon 33: 26-38.

Meacham, C. A. 1986. More about directed characters: A reply to Donoghue and Maddison. Taxon 35: 538-540.

Michener, C. D. 1944. Comparative external morphology, phylogeny, and a classification of the bees (Hymenoptera). Bulletin of the American Museum of Natural History 82: 151-326.

Michener, C. D. 1975. A taxonomic study of African allodapine bees. Bulletin of the American Museum of Natural History 155: 67-240.

Michener, C. D. 1978. The parasitic groups of Halictidae (Hymenoptera: Apoidea). University of Kansas Science Bulletin 51: 291-339.

Michener, C. D. 1979. Biogeography of the bees. Annals of the Missouri Botanical Garden 66: 277-347.

Michener, C. D. 1981a. Classification of the bee family Melittidae with a review of species of Meganomiinae. Contributions of the American Entomological Institute 18(3): i-iii + 1-135.

Michener, C. D. 1981b. Comparative morphology of the middle coxae of Apoidea. Journal of the Kansas Entomological Society 54: 319-326.

Michener, C. D. 1984. A comparative study of the mentum and lorum of bees. Journal of the Kansas Entomological Society 57: 705-714.

Michener, C. D. 1986. A review of the tribes Diphaglossini and Dissoglottini (Hymenoptera, Colletidae). University of Kansas Science Bulletin 53: 183-214.

Michener, C. D. 1989. Classification of American Colletinae (Hymenoptera, Apoidea). University of Kansas Science Bulletin 53: 622-703.

Michener, C. D. 1992. Sexual dimorphism in the glossa of Colletidae. Journal of the Kansas Entomological Society 65: 1-9.

Michener, C. D., and R. W. Brooks. 1984. Comparative study of the glossae of bees (Apoidea). Contributions of the American Entomological Institute 22(1): i-vi + 1-[74].

Michener, C. D., and L. Greenberg. 1980. Ctenoplectridae and the origin of long-tongued bees. Zoological Journal of the Linnean Society [London] 69: 183-203.

Michener, C. D., and D. A. Grimaldi. 1988. The oldest fossil bee: Apoid history, evolutionary stasis, and antiquity of social behavior. Proceedings of the National Academy of Sciences USA 85: 6424-6426.

Michener, C. D., R. J. McGinley, and B. N. Danforth. 1994. The Bee Genera of North and Central America (Hymenoptera: Apoidea). Washington, D. C.: Smithsonian Institution Press. x + 209 pp.

Michener, C. D., and G. Poinar, Jr. In press. The bee fauna of the Dominican amber. Journal of the Kansas Entomological Society.

Nixon, K. M., and J. M. Carpenter. 1993. On outgroups. Cladistics 9: 413-426.

O'Grady, R. T., and G. B. Deets. 1987. Coding multistate characters, with special reference to the use of parasites as characters of their hosts. Systematic Zoology 36: 268-279.

Perkins, R. C. L. 1912. Notes, with descriptions of new species, on aculeate Hymenoptera of the Australian region. Annals and Magazine of Natural History (8)9: 96-121.

Pesenko, Y. A. 1983. Tribe Nomioidini (in the palearctic fauna), pp. 1-199. *In* Fauna of the USSR, Insecta—Hymenoptera, Halictid Bees (Halictidae), Subfamily Halictinae. Leningrad: Nauka. (In Russian.)

Radchenko, V. G., and Y. A. Pesenko. 1994. Biology of Bees (Hymenoptera, Apoidea). St. Petersburg: Russian Academy of Sciences, Zoological Institute. 350 pp. (In Russian, with English summary.)

Rasnitsyn, A. P., and C. D. Michener. 1991. Miocene fossil bumble bee from the Soviet Far East with comments on the chronology and distribution of fossil bees. Annals of the Entomological Society of America 84: 583-589.

Roig-Alsina, A., and C. D. Michener. 1993. Studies of the phylogeny and classification of long-tongued bees. University of Kansas Science Bulletin 55: 124-162.

Rozen, J. G., Jr. 1964. Phylogenetic-taxonomic significance of last instar of *Protoxaea gloriosa* Fox, with descriptions of first and last instars (Hymenoptera: Apoidea). Journal of the New York Entomological Society 72: 223-230.

Rozen, J. G., Jr. 1977. Biology and immature stages of the bee genus *Meganomia* (Hymenoptera, Melittidae). American Museum Novitates No. 2630: 1-14.

Rozen, J. G., Jr. 1984. Nesting biology of diphaglossine bees. American Museum Novitates No. 2786: 1-33.

Rozen, J. G., Jr. 1993. Phylogenetic relationships of *Euherbstia* with other short-tongued bees. American Museum Novitates No. 3060: 1-17.

Rozen, J. G., Jr. 1994. Biologies of the bee genera *Ancylandrena* (Andrenidae: Andreninae) and *Hexepeolus* (Apidae: Nomadinae), and phylogenetic relationships of *Ancylandrena* based on its mature larva. American Museum Novitates No. 3108: 1-19.

Rozen, J. G., Jr., and R. J. McGinley. 1974. Phylogeny and systematics of Melittidae based on mature larvae (Insecta, Hymenoptera, Apoidea). American Museum Novitates No. 2545: 1-31.

Schuberth, J., and K. Schönitzer. 1993. Vergleichende Morphologie der Fovea facialis und der Stirnseitendruse bei Apoidea und Sphecidae (Hymenoptera, Aculeata). Linzer Biologische Beitrage 25: 205-277.

Silveira, F. A. 1993. Phylogenetic relationships of the Exomalopsini and Ancylini (Hymenoptera: Apoidea). University of Kansas Science Bulletin 55: 163-173.

Sober, E. 1988. Reconstructing the Past: Parsimony, Evolution, and Inference. Cambridge, Massachusetts: The MIT Press. 265 pp.

Swofford, D. L. 1993. PAUP: Phylogenetic Analysis Using Parsimony, Version 3.1. Computer program distributed by the Illinois Natural History Survey, Champaign, Illinois.

Swofford, D. L., and D. P. Begle. 1993. PAUP User's Manual. Champaign, Illinois: Center for Biodiversity, Illinois Natural History Survey. vi + 265 pp.

Winston, M. L. 1979. The proboscis of the long-tongued bees: A comparative study. University of Kansas Science Bulletin 51: 631-667.

Zeuner, F. E., and F. J. Manning. 1976. A monograph on fossil bees. Bulletin of the British Museum (Natural History), Geology 27: 151-268, pls. 1-4.

THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. 55, No. 12, pp. 425-454 November 3, 1995

HARVARD UNIVERSITY

Phylogenetic Relationships and Classification of Exomalopsini with a New Tribe Teratognathini (Hymenoptera: Apoidea)[1]

FERNANDO A. SILVEIRA[2,3]

TABLE OF CONTENTS

Abstract 426
Introduction 426
Acknowledgements 427
Material and Methods 427
Selection of Taxa 427
Selection of Characters 427
Descriptions of Transformation Series 428
Analyses 436
Results 436
Cladograms 436
Phylogenetic Relationships among the Outgroups 438
Phylogenetic Relationships within Exomalopsini 440
Classificatory Proposals 449
Tribe Teratognathini 449
Tribe Exomalopsini 449
Genus *Eremapis* 449
Genus *Anthophorula* 449
Subgenus *Isomalopsis*, 449; Subgenus *Anthophorula s.s.*, 450; Subgenus *Anthophorisca*, 450.
Genus *Exomalopsis* 450
Subgenus *Stilbomalopsis*, 450; Subgenus *Phanomalopsis*, 450; Subgenus *Diomalopsis*, 451; Subgenus *Exomalopsis s.s.*, 451.
Key to the Genera and Subgenera of Exomalopsini 451
Discussion and Conclusions 452
Phylogenetic Considerations 452
Biogeographic Considerations 452
Literature Cited 453

[1] CONTRIBUTION NUMBER 3151 FROM THE SNOW ENTOMOLOGICAL MUSEUM, UNIVERSITY OF KANSAS, LAWRENCE.
[2] DEPARTMENT OF ENTOMOLOGY AND SNOW ENTOMOLOGICAL MUSEUM, SNOW HALL, UNIVERSITY OF KANSAS, LAWRENCE, KANSAS 66045, U.S.A.
[3] PRESENT ADDRESS: DEPARTAMENTO DE BIOLOGIA GERAL, INSTITUTO DE CIÊNCIAS BIOLÓGICAS, UNIVERSIDADE FEDERAL DE MINAS GERAIS, C.X.P. 2486, 30161 BELO HORIZONTE, MG, BRASIL.

ABSTRACT

The phylogenetic relationships between Exomalopsini and other apine taxa and among exomalopsine groups are reexamined by means of cladistic analyses. The genera *Teratognatha* Ogloblin and *Chilimalopsis* Toro are removed from Exomalopsini and placed in a new tribe, Teratognathini. A new generic and subgeneric classification is proposed for Exomalopsini based on the results of the phylogenetic analyses. *Anthophorula* Cockerell is raised to generic status, with three subgenera: *Isomalopsis* Michener & Moure, *Anthophorisca* Michener & Moure (including *Panomalopsis* Timberlake new synonym) and *Anthophorula* s.s. *Exomalopsis* Spinola is redefined and divided into four subgenera: *Stilbomalopsis* (proposed here for *Exomalopsis solani* and related species), *Phanomalopsis* Michener & Moure, *Diomalopsis* Michener & Moure and *Exomalopsis* s.s. (including *Megomalopsis* Michener & Moure new synonym). A key is provided for the recognition of these groups.

INTRODUCTION

The tribe Exomalopsini was erected by Michener (1944) and redefined by Michener & Moure (1957) as being composed of 11 genera in 5 sections: 1. *Ancyloscelis*; 2. *Caenonomada*; 3. *Monoeca*; 4. *Exomalopsis, Isomalopsis, Teratognatha* and *Eremapis* and 5. *Chalepogenus, Lanthanomelissa, Tapinotaspis* and *Paratetrapedia*. A new genus, *Chilimalopsis*, was described by Toro (1976) and was said to be allied to *Exomalopsis*. In a recent phylogenetic study of the long-tongued bees, Roig-Alsina & Michener (1993) removed all but group 4 from Exomalopsini. Subgenera of *Exomalopsis* will be used in the sense of Michener & Moure (1957) in the following discussion, and a revised grouping will be proposed in the section on classification.

Eremapis, Teratognatha and *Isomalopsis* are all monospecific groups; *Chilimalopsis* contains two species. All these groups are confined to the semidesertic areas of temperate South America, which is believed to be the center of origin for Exomalopsini (Michener, 1944). *Exomalopsis*, on the other hand, is widespread through the western hemisphere, occurring in deserts, tropical savannas and forests and in temperate prairies between 41° South and 42° North. There is considerable morphological diversity in *Exomalopsis* which has been reflected in the taxonomy of the genus. Cockerell (1897b) erected the genus *Anthophorula*, which he later considered to be a subgenus of *Exomalopsis* (*e.g.*, Cockerell, 1899). Michener & Moure (1957) recognized six subgenera (*Anthophorisca, Anthophorula, Phanomalopsis, Diomalopsis, Megomalopsis* and *Exomalopsis s.s.*). An additional subgenus, *Panomalopsis*, was erected by Timberlake (1980) to include one distinctive species.

Little is known about the biology of exomalopsine bees. Nests of the following species have been studied: *Eremapis parvula* (Neff, 1984), *Exomalopsis (Anthophorula) crenulata* (Parker, 1984), *E. (Anthophorula) torticornis* (Hicks, 1936), *E. (Anthophorisca) chionura* (Rozen & McNeil, 1957; Rozen, 1984), *E. (Anthophorisca) consobrina* (Rozen, 1977), *E. (Anthophorisca) sidae* (Rozen, 1984), *E. (Phanomalopsis) solidaginis* (Rozen, 1984), *E. (Phanomalopsis) solani* (Linsley *et al.*, 1954; Rozen, 1984; Norden *et al.*, 1994), *E. (Exomalopsis) auropilosa* (Zucchi, 1973) and *E. (Exomalopsis) pulchella* and *E. (Exomalopsis) similis* (Raw, 1977).

Eremapis seems to construct only a single cell per nest (Neff, 1984), which suggests that it is solitary. All studied species of *Exomalopsis s.l.*, on the other hand, seem to have more than one female to a nest. One nest of *Exomalopsis auropilosa* contained 884 females (Zucchi, 1973)! Michener (1966) suggested that cooperative provisioning may occur in *E. solani*. Raw (1977) suggested that *Exomalopsis pulchella* and *E. similis* are quasisocial or, perhaps, semisocial.

The foraging habits in the tribe are variable. Some species seem to be oligoleges (*e.g., Eremapis parvula* on *Prosopis* (Fabaceae)—Neff, 1984; *Exomalopsis pygmaea* on *Helianthus annuus* (Asteraceae)—Hurd *et al.*, 1980; others take their food from a wide range of plant species (*e.g., Exomalopsis auropilosa, E. similis, E. solani*—Camargo & Mazucato, 1984; Raw, 1976; Timberlake, 1980; Silveira *et al.*, 1993).

The phylogeny of the exomalopsine genera and their relationships with other bee taxa are not well understood. Exomalopsini has been considered traditionally to be among the most ancient stocks of the Anthophorinae (*e.g.*, Michener, 1944; Michener & Moure, 1957) and to be related to the palaearctic genera *Pararhophites, Ancyla* and *Tarsalia* (Michener, 1944, 1979; Michener & Moure, 1957). Ideas of relatedness at the time these hypothesis were proposed, however, were commonly influenced by presence of shared plesiomorphies, and groups believed to be related then may not constitute monophyletic groups in the sense of Hennig (1966). The tribe Pararhophitini was erected by Popov (1949) for *Pararhophites*, which was later (McGinley & Rozen, 1987; Roig-Alsina & Michener, 1993) demonstrated to be part of the megachilid lineage. *Ancyla* and *Tarsalia* were grouped in the Ancylini by Michener (1944). This systematic arrangement has been generally accepted, and the question remained as to whether or not Ancylini was allied to or a synonym of Exomalopsini (*e.g.*, Popov, 1949; Michener & Moure, 1957; Michener, 1979; McGinley & Rozen, 1987). A close relationship between the Ancylini and the Exomalopsini was supported by some of the trees obtained by Silveira (1993), but there were equally parsimonious trees in which these tribes were not sister taxa.

The first cladistic analyses to include genera of Exomalopsini were those of Roig-Alsina & Michener's (1993) study of the phylogeny of the long-tongued bees. Their results suggest that Exomalopsini would be a paraphyletic assemblage at the base of the Apinae (*sensu* Roig-Alsina & Michener, 1993; these authors do not recognize Anthophorinae as a taxon and place all genera previously assigned to it in the subfamily Apinae). In their trees, *Eremapis* was the first taxon within Exomalopsini to branch off, followed by *Teratognatha* and *Isomalopsis* plus *Exomalopsis*. In a paper com-

plementary to that of Roig-Alsina & Michener, Silveira (1993) used their data to address the relationships of Exomalopsini with other Apinae but did not reach conclusive results. His analyses suggested that Exomalopsini could either be a paraphyletic group at the base of Apinae (as in Roig-Alsina & Michener's results) or a monophyletic group with uncertain relationship to the other tribes of Apinae. *Chilimalopsis* was not included in either Roig-Alsina & Michener's (1993) or in Silveira's (1993) studies.

Here, the phylogenetic relationships between Exomalopsini and other tribes of Apinae are reexamined, and the phylogeny of the exomalopsine genera studied by means of cladistic analyses. The generic classification of Exomalopsini and the subgeneric classification of *Exomalopsis* are revised.

ACKNOWLEDGMENTS

This paper is part of a dissertation presented as partial requirement for the degree of PhD at the Department of Entomology of the University of Kansas and was made possible by a scholarship granted to me by the Brazilian council for development of science and technology (CNPq). I am indebted to B.A. Alexander, C.D. Michener and G.A.R. Melo for their continuous interest in this project. Their support, criticisms and suggestions were of great help to the completion of this paper. I also benefited from talking with J.S. Ash about cladistic analyses and related subjects. The execution of this work would not be possible without the bees lent to me by different institutions. I am very grateful to these institutions and their curators named in Material and Methods. Douglas Yanega was kind enough to allow me to use his templates to draw the phylogenetic trees presented here.

MATERIAL AND METHODS

Selection of Taxa

All known species of *Teratognatha, Chilimalopsis, Eremapis* and *Isomalopsis* were included in the phylogenetic analysis. *Exomalopsis s.l.* (*sensu* Michener & Moure, 1957), however, includes some 150 species. The inclusion of all of them in this study would be impractical, not only because they would make the data matrix enormous, but also because not all of them were available for study. For this reason a sample of species was taken to represent the geographical and morphological diversity of the group. Material available for the subgenera *Exomalopsis*, *Megomalopsis* and *Phanomalopsis* (*sensu* Michener & Moure, 1957) was sorted to morphospecies and identified as far as possible. During this process, the species were grouped according to the presence of features believed to be synapomorphic. From each of these groups at least two species were selected for which enough material was available for study and which would represent the geographical distribution of the groups and of the genus. The representatives of *Anthophorula* and *Anthophorisca* were chosen based on the main groups defined by Timberlake's (1980) keys. The only known species of *Diomalopsis* was also included. However, the subgeneric name *Panomalopsis* is based on a single male and, for this reason, was not included in the matrix.

The outgroups were chosen according to the findings of Roig-Alsina & Michener (1993) and Silveira (1993). Two representatives each of Ancylini, Eucerini, Emphorini, Tapinotaspini and Xylocopinae and one representative of Tetrapediini, Ctenoplectrini and Nomadinae were employed. The taxa used in the analyses are listed in Table I.

Specimens examined for the construction of the data matrix received a green label "F.A.Silveira – Exomalopsini Relationships". Most of them are deposited at the Snow Entomological Museum of the Natural History Museum of the University of Kansas. Specimens of *Ancyla* spp., *Chilimalopsis impressifrons, Exomalopsis euphorbiae, E. completa,* and *E. sidae* are in the American Museum of Natural History, New York, U.S.A. (J.G.Rozen and E. Quinter); specimens of *Eremapis parvula, Isomalopsis niveata* and *Exomalopsis analis* are in the Instituto Miguel Lillo of the Universidad Nacional de Tucumán, Tucumán, Argentina (A. Willink); specimens of *Monoeca* cf. *brasiliensis, Exomalopsis fulvofasciata, E. auropilosa, E. analis* and *E. vernoniae* are in the Museu Regional de Entomologia da Universidade Federal de Viçosa, Viçosa, Minas Gerais, Brazil (P.S.F.Fiuza); specimens of *Exomalopsis vernoniae* are in the Department of Entomology, Michigan State University, East Lansing (F.W. Stehr, V. Scott); specimens of *Exomalopsis similis, E. pulchella* and *Isomalopsis niveata* are in the Los Angeles County Museum of Natural History (R. R. Snelling); specimens of *Exomalopsis analis* and *E. tepaneca* are in the Museo de Zoología "Alfonso L. Herrera" of the Universidad Nacional Autonoma de México, Ciudad México, México (L.Godinez); specimens of *Exomalopsis vernoniae* are in the Museu de La Plata, La Plata, Argentina (Ricardo Ronderos); specimens of *E. auropilosa* are in the Bee Biology and Systematics Laboratory, Logan, Utah, U.S.A. (T.L. Griswold).

Since no definitive conclusions could be reached by Roig-Alsina & Michener (1993) or Silveira (1993) about the relationships between Exomalopsini and other groups of Apinae, I preferred not to constrain the analysis to any of the specific cladograms discussed in those papers. Instead of polarizing the characters beforehand, as did Silveira (1993), I allowed the analyses to indicate the most parsimonious arrangements for Exomalopsini and the other groups, as suggested by Nixon & Carpenter (1993) and used Xylocopinae (*Manuelia* + *Xylocopa*) to root the trees.

Selection of Characters

Characters appearing in only one of the species employed in the analyses were excluded from the cladistic analyses since they would not convey phylogenetic information. Quantitative continuous characters were generally (but not completely) avoided. Coding for such characters will be discussed in the description of individual characters below.

Only characters believed to be independent of other characters were employed. The presence of yellow or white marks on face of male bees has been used as a single character. The observation that yellow marks can be independently present in different parts of the face (labrum, clypeus, supraclypeal area etc.) prompted me to divide this feature into several characters (numbers 15 - 20, below). The same was done regarding the presence and distribution of tomentum on metasomal terga 1 to 4 (characters 52 - 55, below).

Only external morphological characters were employed here. Furthermore, search for characters was limited to adult females and males, since immature stages are unknown for the large majority of species in the tribe. Many characters are present only in one sex as pointed out in their descriptions below. All characters for which no sex is specified are coded based on the female. Although they are known or presumed to be common for both sexes, this may not be true for all of them.

Explanations are needed as to how some characters were interpreted and named:

A sparse and regularly spaced line of erect hairs is present along the inner margin of the eyes in *Exomalopsis* (*sensu* Michener & Moure, 1957). This row of hairs is referred to, below, as the *paraoc-*

Table I. Taxa employed in the phylogenetic analyses. Generic and subgeneric classification of Exomalopsini according to Michener & Moure (1957).

OUTGROUPS	TETRAPEDIINI	*E. (Exomalopsis) analis* Smith
XYLOCOPINAE	*Tetrapedia clypeata* Friese	*E. (Exomalopsis) auropilosa* Spinola
Manuelia gayi (Spinola)		*E. (Exomalopsis) bruesi* Cockerell
Xylocopa virginica (Linnaeus)	**INGROUP**	*E. (Exomalopsis) campestris* Silveira
NOMADINAE	*Chilimalopsis* sp. (from Chile)	*E. (Exomalopsis) mourei* Michener
Nomada snowii Cresson	*C. impressifrons* Roig-Alsina	*E. (Exomalopsis) pulchella* Cresson
ANCYLINI	*Eremapis parvula* Ogloblin	*E. (Exomalopsis) similis* Cresson
Ancyla oraniensis Lepeletier	*Teratognatha modesta* Ogloblin	*E. (Exomalopsis) tomentosa* Friese
Tarsalia ancyliformis Popov	*Isomalopsis niveata* (Friese)	*E. (Exomalopsis) vernoniae* Schrottky
EUCERINI	*E. (Anthophorisca) consobrina* Timberlake	*E. (Megomalopsis) fulvofasciata* Smith
Eucerinoda gayi (Spinola)	*E. (Anthophorisca) micheneri* Timberlake	*E. (Megomalopsis) mellipes Cresson*
Melissodes agilis Cresson	*E. (Anthophorisca) pallidicornis* Timberlake	*E. (Phanomalopsis) aureosericea* Friese
EMPHORINI	*E. (Anthophorisca) pygmaea* (Cresson)	*E. (Phanomalopsis) birkmanni* Cockerell
Ancyloscelis apiformis (Fabricius)	*E. (Anthophorisca) sidae* Cockerell	*E. (Phanomalopsis) byersi* Timberlake
Ptilothrix tricolor (Friese)	*E. (Anthophorisca) texana* Friese	*E. (Phanomalopsis) jenseni* Friese
CTENOPLECTRINI	*E. (Anthophorula) albata* Timberlake	*E. (Phanomalopsis) snowi* Cockerell
Ctenoplectra fuscipes (Friese)	*E. (Anthophorula) compactula* Cockerell	*E. (Phanomalopsis) solani* Cockerell
TAPINOTASPINI	*E. (Anthophorula) completa* Cockerell	*E. (Phanomalopsis) solitaria* Brèthes
Paratetrapedia lugubris (Cresson)	*E. (Anthophorula) euphorbiae* Timberlake	*E. (Phanomalopsis) trifasciata* Brèthes
Monoeca cf. *brasiliensis* Lepeletier & Serville.	*E. (Diomalopsis) bicellularis* Michener & Moure	

ular cilia. It is present both in female and males, although in the latter it is sometimes disguised by the long hairs on the paraocular areas.

The term vertex has been used in the bee literature just as a descriptive word referring to the dorsalmost region of the head. Working with *Exomalopsis*, however, makes it necessary to make a more precise definition for the region between the ocelli and the occiput (from here on, *postocellar region*), to avoid confusion between non-homologous structures. In most bees, the occiput and postocellar region can be distinguished by a more or less abrupt change in punctation and pilosity. Frequently they are separated by a preoccipital ridge or carina. The meeting between the the two regions may occur at the summit of the head or behind it, on the back of the head. In the Exomalopsini, the region corresponding to the vertex of most bees is bent backward and downward bringing the ocelli to the summit of the head and part or all the postocellar region to the back of the head (Fig.1b,c). In the past, it was usual for authors to refer to the more or less sharp ridge on the summit of the head of *Exomalopsis s.s.* and *Megomalopsis* (both *sensu* Michener & Moure, 1957) as the preoccipital carina. This ridge, however, is clearly not homologous with the preoccipital carinae of other bees, since it is well before the vertex-occipital line. In fact, some Exomalopsini (*e.g., Isomalopsis niveata* and *Anthophorula albata*) have a true preoccipital carina on the back of their heads, a feature that apparently was not noticed by previous taxonomists (Fig.1b). For this reason, I will refer to the structure on the head of *Exomalopsis s.s.* and *Megomalopsis* as the *postocellar ridge* and to the arrangement of hairs referred to as occipital fringe by Timberlake (1980) as the *postocellar fringe.*

Medially, on the posterior margin of the propodeum, there is a special, somewhat strengthened area delimiting the articulating orifice of the propodeum (Fig.5 *ao*) and producing the propodeal teeth described by Michener (1944). This area is here named 'propodeal crescent' (Fig. 5 *cr*).

Many *Exomalopsis* have a shallow transverse depression that divides the dorsal surface of tergum I into an anterior and a posterior zone. Michener & Moure (1957) used this depression as a diagnostic character for their subgenera *Megomalopsis* and *Phanomalopsis.* This depression coincides with the premarginal line (Michener *et al.*, 1994), which separates the disc from the marginal area of the tergum (Michener, 1944; = posterior marginal depression of Camargo *et al.*, 1967; = apical depression of Timberlake, 1980). Strong evidence that the transverse depression is homologous to the premarginal line is the fact that, when present, it indicates the insertion of the intersegmental membrane on the internal surface of the tergum. This is the same for the premarginal line of other bees (Camargo *et al.*, 1967; Silveira, unpublished observations).

Descriptions of Transformation Series

The term character is used here, following Wiley *et al.* (1991), to designate the attribute of a given species (referred to by authors as character state). The set of alternative homologous characters (referred to by authors as character) is designated here as a trans-

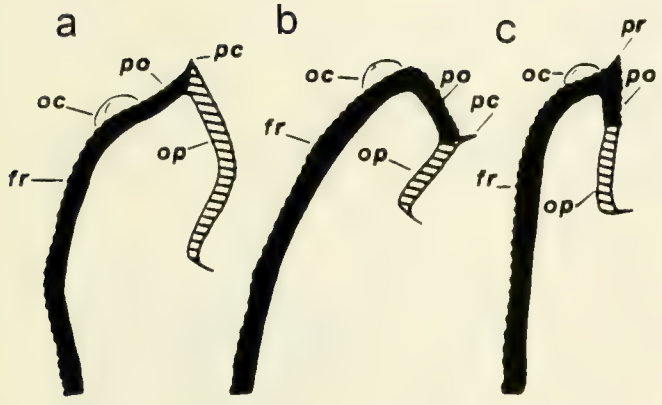


Fig. 1. Sagittal sections of heads of bees (schematic) showing hypothesized change in relative positions of postocellar region and occiput (see text for explanation). (**a**) as in *Monoeca cf. brasiliensis*; (**b**) as in *Exomalopsis* (Anthophorula) albata*; (**c**) as in *Exomalopsis (Megomalopsis**) fulvofasciata*. *fr* = frons; *oc* = median ocellus; *op* = occiput; *po* = postocellar region; *pc* = preoccipital carina; *pr* = postocellar ridge. * *Anthophorula* in the classification proposed here. ** *Exomalopsis* in the classification proposed here.

formation series. Transformation series containing more than two characters (multistate characters of authors) were not ordered, and their numbers should not be taken to imply plesiomorphic or derived conditions. In one instance, mixed coding (as explained in Wiley *et al.*, 1991), which is a way to order characters, was employed. This was done by the use of transformation series 61 and 62 to code for variations in two of the characters in transformation series 60. Outside the ingroup, while most of the characters recorded probably do not vary greatly within any one genus, the data are based only on the exemplars listed in Table I.

When many characters were present in a single transformation series, a detailed codification would take more than the 10 characters acceptable by parsimony programs such as Hennig86. The solution I found was to codify those characters that appeared in more than one taxon, ignoring some features occurring only in a single species among the outgroups (which were coded as the common character). The shape of disc of sternum VII of male (transformation series 60) is one example of a series in which unique characters were coded as the common feature 'triangular'. Since these unique characters would show up in the results as autapomorphies for the species in which they appear, ignoring them does not influence the topology of the cladograms obtained.

Metasomal terga and sterna are referred to, respectively, as T-1, T-2, etc. and S-1, S-2, etc.

1: Base of first labial palpomere (0) parallel sided; (1) with a constriction on inner side [Fig.16 in Roig-Alsina & Michener, 1993].

2: Mandibles (0) simple; (1) with inner subapical tooth.

3: Posterior mandibular articulation (0) even with posterior margin of eye; (1) anterior to posterior margin of eye.

4: Disc of labrum of female (0) flat [Fig.2a]; (1) concave [Fig.2b]; (2) convex. *Manuelia* and *Xylocopa* have the labrum relatively reduced with a large portion represented by the basal polished area. I consider the small remaining portion, which is convex, as the disc of the labrum. I am not sure, however of the homology relative to the labrum of other bees. *Tetrapedia* has the longitudinal median area depressed and the apical margin bent forward. Perhaps it should be considered as a different character, but I consider that the disc of the labrum is flat (coded 0). *Eucerinoda* also has a median depression on the labrum, but the disc as a whole is not concave (coded 0).

5: Apical edge of labrum of female (0) straight or gently curved (sometimes with a median knob) [Fig.2a]; (1) pointed [Fig.2b]. *Tetrapedia* has a specialized labrum in which the apical edge has two median denticles (coded 0). *Eucerinoda* does have a median angle on the edge. However it looks more like a projection of the disc over the edge (like the median knob of other bees), rather than part of the edge itself (coded 0). In *Ptilothrix*, the labrum is conspicuously acuminate and is coded as such. However, the apical margin is very specialized, suggesting that it is not homologous to other pointed labra such as those in the *Exomalopsis jenseni* group. *Isomalopsis* has a relatively long labrum. The lateral portions of its apical edge do converge, but in a gentle curve, which is truncated at the apex (coded 0).

6: Longitudinal median line of female labrum (0) undifferentiated; (1) glabrous, sometimes elevated in relation to rest of disc; (2) glabrous, sometimes elevated; delimited by 2 rows of hairs [Fig.2a]. *Eucerinoda* has a median glabrous area that is incomplete, starting far from the labral base (coded 1). In *Isomalopsis* the median line is very broad (coded 0). In *Exomalopsis birkmanni*, the two lines of hairs delimiting the median line are obliterated by a tuft of hair on each side (coded 2).

7: Anterior surface of labrum of female (0) with basal polished area; (1) without basal polished area. *Ctenoplectra fuscipes* has a thick, glabrous ridge that suggests a degenerated basal polished area. No

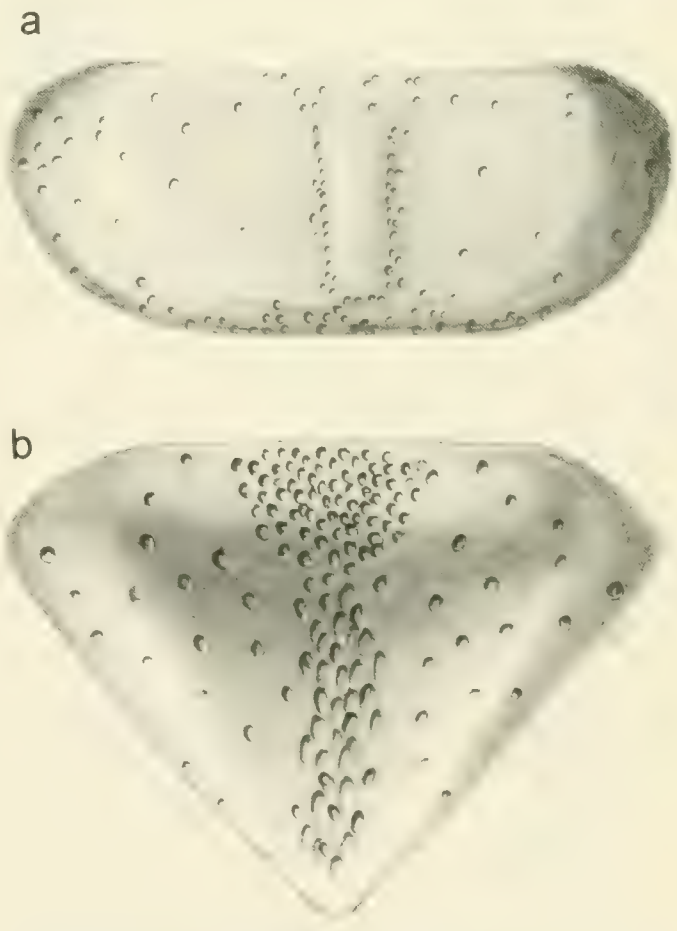


Fig. 2. Labra of (**a**) *E. (Exomalopsis) auropilosa* and (**b**) *Exomalopsis (Phanomalopsis) snowi*.

other species in the genus has it, although some others have other features suggesting the basal area (coded 0). *Teratognatha* has a flattened basal area that, for the most part, lacks punctation. It is not much elevated and was not considered as homologous to the basal area in bees such as *Xylocopa* and *Ancyla*.

8: Outline of summit of head of female, in frontal view, (0) uniformly convex [Fig.3a]; (1) in straight line between eye and ocellus [Fig.3b]. The summit of the head in *Ancyla* is very gently convex, almost straight, but was coded as 0.

9: Lateral profile of vertex of female, between eye and lateral ocellus: (0) convex [Fig.1b]; (1) excavated [Fig.1a,c]. In *Xylocopa*, the ocelli are very low, relative to the summit of the head, and the vertex is almost level between the ocellus and the eye (coded 0).

10: Summit of head of female, in dorsal view, (0) distant from lateral ocelli (one ocellar diameter or more behind lateral ocelli); (1) close to lateral ocelli (less than one ocellar diameter behind lateral ocelli).

11: Postocellar region of female, behind summit of head, (0) convex in lateral profile [Fig.1a,b]; (1) plane or concave in lateral profile [Fig.1c]. In *Nomada*, the vertex does not bend down before meeting the occiput, but still is convex (coded 0). In *Paratetrapedia lugubris*, the summit of the head coincides with the preoccipital carina (coded 0). In *Exomalopsis aureosericea* and *E. michener* the postocellar region is only very gently convex, behind the summit of the head, but was still coded as 0. *Exomalopsis completa* has the postocellar region ending just behind the summit of the head. The short portion on the back of the head, however, is convex.

12: Superior margin of eye of female, in frontal view, (0) below summit of head [Fig.3a]; (1) above summit of head [Fig.3b].

13: Lateral ocelli of female, in frontal view, (0) entirely below summit of head behind them [Fig.3a]; (1) at least partially above summit of head [Fig.3b].

14: Paraocular cilia of female (0) absent; (1) present.

15: Mandibles of male (0) entirely dark; (1) with yellow pigmented area at least at base. In most Exomalopsini the male mandibles are black, sometimes with parts (especially at the apex) brown to bright ferrugineous. State one refers to pale to bright yellow maculae, as are sometimes found on the labrum and clypeus.

16: Labrum of male (0) entirely dark; (1) with yellow pigmented area.

17: Clypeus of male (0) entirely dark; (1) with yellow pigmented area.

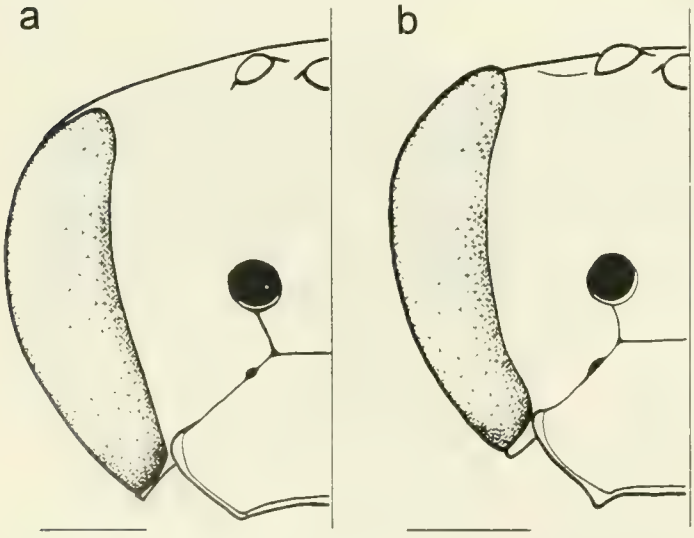


Fig. 3. Frontal views of heads of (**a**) *Exomalopsis (Phanomalopsis*) burkmanni* and (**b**) *E. (Exomalopsis) auroplosa*. Scale lines = 0.50 mm. * *Stilbomalopsis* in the classification proposed here.

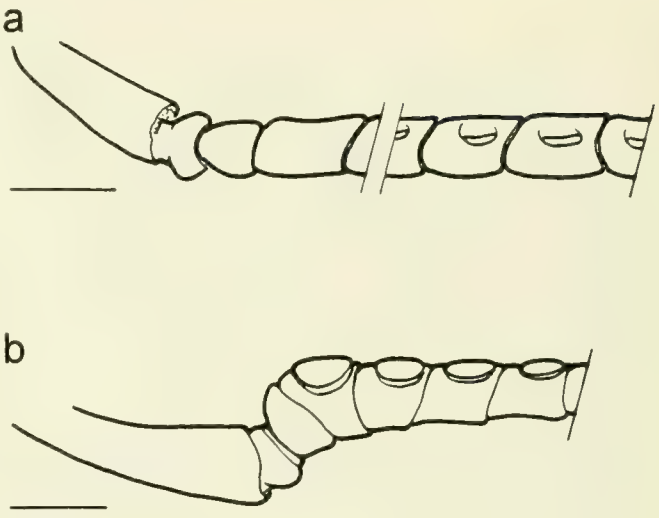


Fig. 4. Antennae of males of (**a**) *Exomalopsis* (Anthophorula) albata* and of (**b**) *Exomalopsis* (Anthophorula) completa*. Flagellomeres 3 (part), 4, 5 (part), 8(part), 9, 10 and 11 in (a) and flagellomeres 6 (part) to 11 in (b) are omitted. Scale lines = 0.25 mm. * *Anthophorula* in the classification proposed here.

18: Paraocular area of male (0) entirely dark; (1) with yellow pigmented area.

19: Supraclypeal area of male (0) entirely dark; (1) with yellow pigmented area.

20: Scape of male (0) entirely dark; (1) with yellow pigmented area.

21: Male flagellomeres (0) entirely dark (ferrugineous to black); (1) at least one yellow pigmented ventrally. *Teratognatha* has pale ferrugineous flagellomeres (coded 0).

22: Male flagellomeres (0) simple; (1) with longitudinal carina on outer side [Fig.4a], which sometimes expands to form a pad [Fig.4b]. *Tetrapedia* and *Ctenoplectra* have a 'swollen' area on the line between the dorsal and ventral surfaces of the antennae. However, this does not constitute a marked edge and, thus, was coded as 0. In *Tarsalia*, the 'carina' is not very well developed but is sharply marked (coded 1).

23: Male flagellum (0) normal; (1) bulging at base, out of alignment with scape, due to an asymmetry in second flagellomere [Fig.4b].

24: First flagellomere of male (0) less than three-fourths of length of second; (1) about as long as second; (2) longer than second.

25: Posterior margin of propodeum (0) continuously separated from disc of propodeum by submarginal groove of propodeum (described by Michener, 1944) [Fig.5d,e, *sg*]; (1) compressed against disc of propodeum so that submarginal groove is interrupted at sides of propodeal crescent [Fig.5a,b]. In *Nomada*, *Melissodes* and *Chilimalopsis sp.*, there is a process of the disc of the propodeum, on each side of the propodeal crescent, which touches the posterior margin, thus interrupting the groove, which continues afterwards, in the medial part of the margin (coded 0). In *Ancyla*, the groove is closed by the propodeal crescent (coded 1).

26: Propodeal articulating orifice (0) directed backward or slightly upwards [Fig.5a,b, *ao*]; (1) directed downwards in an oblique plane [Fig.5d,e, *ao*].

27: Carina on posterior margin of propodeum (0) interrupted medially [Fig.5a,b,d,]; (1) continuous [Fig.5c,e]. In *Xylocopa* and *Nomada* the carina looks as if it had been bent backward and downward on the sides (coded 0). Perhaps this would justify another character. In *Melissodes* the carina continues on top of the crescent as a faint wrinkle (coded 1). In *Exomalopsis similis* there

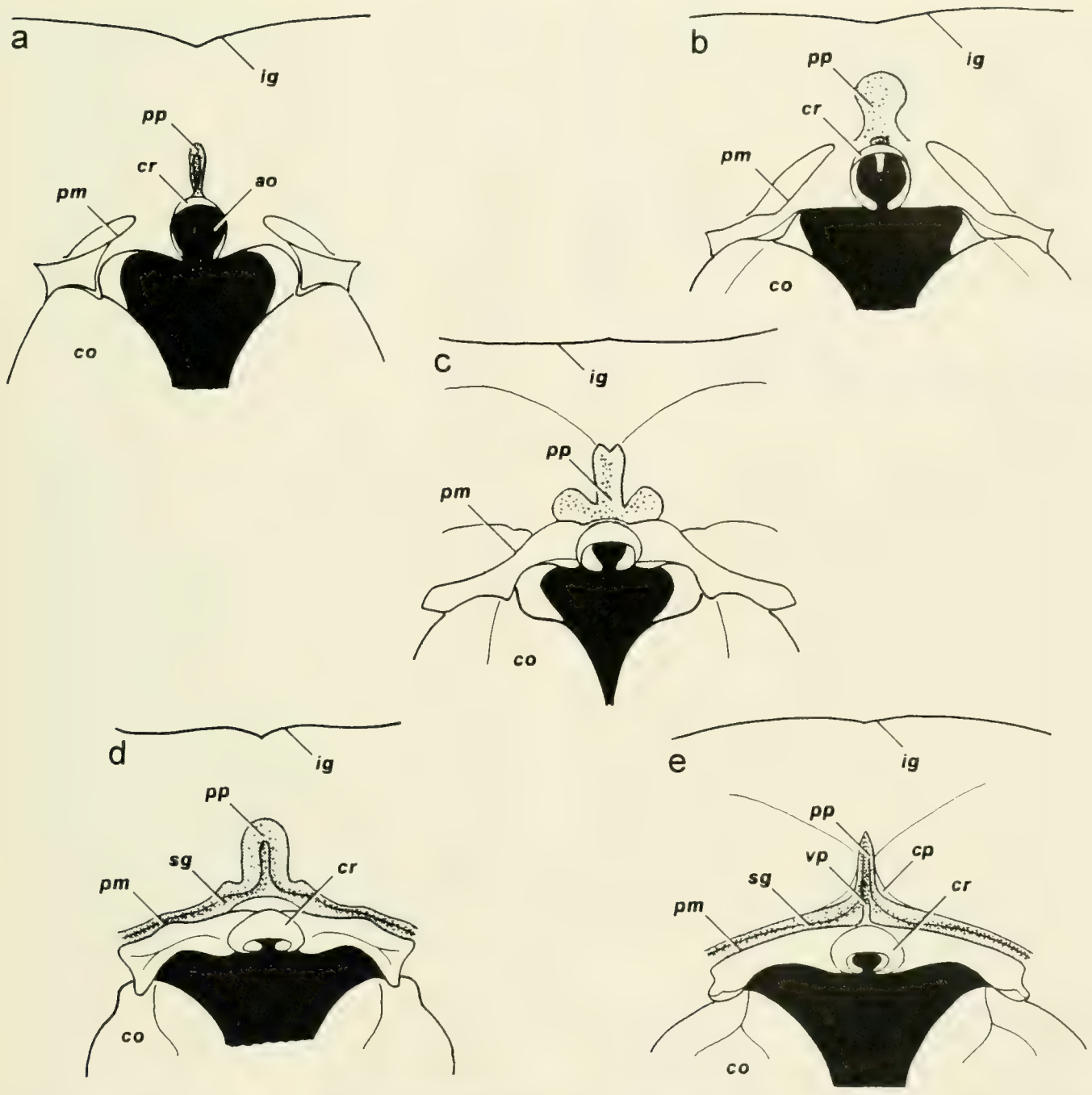


Fig. 5. Posterior view of propodeum of (**a**) *Paratetrapedia lugubris*; (**b**) *Ptilothrix tricolor*; (**c**) *Melissodes agilis*; (**d**) *Exomalopsis (Phanomalopsis) jenseni*; (**e**) *E. (Exomalopsis) analis*. *ao* = articulating orifice of propodeum; *co* = coxa; *cp* = lateral carina of propodeal pit; *ig* = metanotal-propodeal groove; *pm* = posterior margin of propodeum; *pp* = propodeal pit; *cr* = propodeal crescent; *sg* = submarginal groove of propodeum; *vp* = median vertical projection. Stippled areas are impressed into wall of propodeal disc.

is a very reduced line over the crescent (coded 1).

28: Carina on posterior margin of propodeum (0) simple [Fig.5c]; (1) with median vertical projection [Fig.5e, *vp*]. *Exomalopsis bruesi* and, perhaps, *Exomalopsis auropilosa* are polymorphic for this character.

29: Apical third of propodeal triangle, above propodeal pit, (0) with well delimited, shining, non-punctate area; (1) punctate as remainder of propodeum or reticulate. In *Eremapis*, there is some faint indication of reticulation, but the surface is shiny and, to a great extent, smooth (coded 0).

30: Propodeal pit (0) broad and/or with its lateral walls gently slanting toward midline [Fig.5a,b,c,d, *pp*]; (1) a narrow groove, with its lateral walls almost perpendicular to its floor [Fig.5e, *pp*].

31: Submarginal groove of propodeum (0) not or very gently

impressed into wall of propodeal disc [Fig.5a,b]; (1) clearly impressed into wall of propodeal disc and merging with propodeal pit [Fig.5d, *sg, pp*]; (2) as in (1), above, but with a carina above groove on each side of propodeal pit [Fig.5e, *cp*]. In *Paratetrapedia* and *Melissodes*, the groove is deeply impressed, but only for a very short distance on each side of the propodeal crescent, not reaching the propodeal pit [Fig.5a,c] (coded 0).

32: Propodeum, in profile, (0) with a nearly horizontal basal zone, behind which it abruptly turns downward to form declivous posterior surface; (1) entirely slanting or declivous.

33: Membrane closing space behind metasternum and hind coxae and extending to base of metasomal S-1 (0) arising above free apex of metasternum on ridge between hind coxal condyles [Fig.23a,b in Roig-Alsina & Michener, 1993]; (1) arising from apical margin of metasternum, which therefore is not free [Fig.23c in Roig-Alsina & Michener, 1993].

34: Apex of marginal cell (0) on wing margin; (1) rounded or pointed, separating from wing margin in a gentle curve; (2) obliquely truncate, separating from wing margin in a straight line [Fig.6a,b]. In *Paratetrapedia* the cell first recedes from the wing margin in a gentle curve and then continues in a straight line (coded 1).

35: Inner breadth of pterostigma (0) much greater than breadth of marginal veins of pterostigma [Fig.6b]; (1) equal to or less than breadth of marginal veins of pterostigma [Fig.6a, *mv*].

36: Pterostigma (0) at least three times as long as prestigma [Fig.6b]; (1) less than three times as long as prestigma [Fig.6a].

37: Cross vein *cu-v* of forewing meeting vein *m+cu* (0) basad of or at vein *m*; (1) distal to vein *m*. The meeting of *cu-v* and *m+cu* was considered to be at *m* whenever any superposition between *cu-v* and *m* existed on *m+cu*.

38: Ventral surface of front coxa of female (0) with pilosity similar to that on rest of venter of thorax; (1) covered by densely plumose tomentum; (2) covered by thin, short, simple, decumbent hair. In *Anthophorula compactula* and *A.completa* the tomentum is not as dense as in other species (coded 1).

39: Basitibial plate of female (0) flat; (1) with central velvet-like pilose area separated by groove from raised margin.

40: Scopa on hind leg of female (0) dense, with hairs coarsely plumose to apex or nearly so; (1) dense, with mixture of long, simple hairs and shorter, plumose ones; (2) dense, constituting solely of stiff simple hairs; (3) sparse, with hairs minutely and sparsely branched. In *Ptilothrix*, the rachis of each hair is very long and stiff and its branches are very thin and restricted to the basal half of the rachis. This arrangement superficially resembles character (1) but was coded 0.

41: Hind basitarsus of female (0) giving rise to second tarsomere at apex; (1) projecting distad, above articulation of second tarsomere, as process without an apical brush; (2) projecting distad as in (1), but ending in a dense brush (penicillus). In *Ctenoplectra*, the projection is topped by a fine, long and thin brush (coded 1). In Roig-Alsina & Michener (1993), *Paratetrapedia* is coded 1 and *Monoeca* coded 0. The species of *Paratetrapedia* I studied has the structure of the hind basitarsus very similar to that of *Monoeca* and both were coded 0. *Eremapis* is coded as 1 in Roig-Alsina & Michener's paper. My interpretation, however, is that, although very reduced, both the projection and the penicillus are present (coded 2).

42: Hind basitarsus of female (0) narrow (measured at its apex, narrower than tibia and not more than 3 times as broad as second tarsomere), more or less round in cross-section; (1) broad (as broad as or [usually much] broader than tibia and much more than 3 times as broad as second tarsomere), flat. In *Exomalopsis*, the hind basitarsus is narrow, but somewhat flat (coded 0).

43: Trunk of anterior tibial spur (0) simple [Fig.7a]; (1) with expansion at right angle to velum, curving apically into spine of malus [Fig.7b]; (2) with strong expansion at right angle to velum, ending in strong angle [Fig.7c]; (3) with strong expansion as in (2) above, but ending in spine [Fig.7d].

44: Dorsal surface of T-1 (0) clearly shorter than exposed surface of T-2; (1) about as long as or longer than exposed surface of T-2.

45: T-1 of female (0) without transverse carina; (1) with a transverse carina marking boundary between anterior vertical surface and dorsal surface. *E. micheneri, E.pygmaea* and *E. texana* have a weak carina (coded 1).

46: Premarginal line (0) parallel to posterior margin of tergum; (1) arching forward between dorsolateral convexities (most easily seen on T-1, but occurring also at least on T-2 and T-3). The premarginal line is not visible in *Xylocopa*. In *Tarsalia*, it is not very clear, but was coded 1. In *Ptilothrix*, it is obvious only on T-2. In *Chilimalopsis* and *Eremapis*, the arc is very subtle (coded 1).

47: Premarginal line of T-1 of female (0) simple; (1) depressed, forming transverse sulcus. In *E. albata, E. compactula* and *E. completa*, the marginal area is depressed (see character 48) and the premarginal line is below the level of the disc (coded 0). In *E. fulvofasciata* and *E. mellipes*, the sulcus is very weak, as compared with that in *E. byersi*, for instance (coded 1).

48: Marginal area of T-1 of female, at midline (0) at same level as disc; (1) depressed in relation to disc.

49: Disc of T-1 of female, measured lengthwise at midline, (0) longer than marginal area; (1) shorter than but not less than one-third as long as marginal area; (2) less than one-third as long as marginal area. In *Manuelia, Xylocopa* and *Nomada*, the premarginal line is difficult to see and the boundaries between the disc and the marginal area of the tergum are difficult to delimit (coded ?).

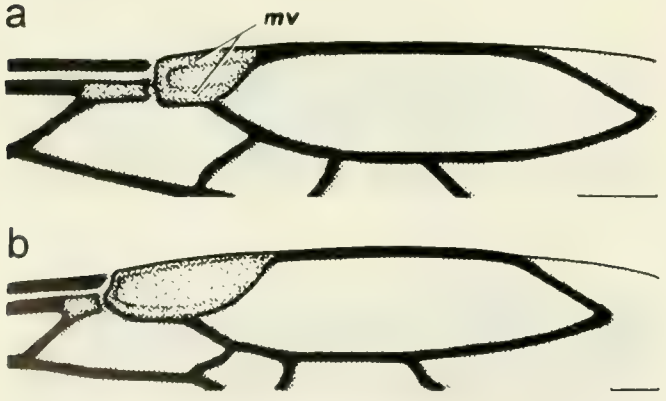


Fig. 6. Portion of front wing of (**a**) *Exomalopsis* (Anthophorula) completa*; (**b**) *E. (Exomalopsis) fulvofasciata*. *mv* = marginal veins of pterostigma. Scale lines = 0.25 mm.

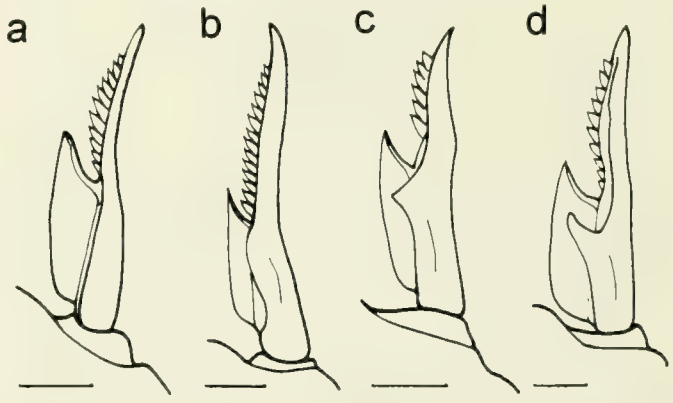


Fig. 7. Anterior tibial spur of (**a**) *Ancyloscelis apiformis*; (**b**) *Tarsalia ancyliformis*; (**c**) *Exomalopsis (Anthophorula) compactula*; (**d**) *E. (Exomalopsis) fulvofasciata*. Scale lines = 0.10 mm.

50: Disc of T-1 of female on dorsal surface, between dorsolateral convexities, (0) punctate; (1) largely impunctate, sometimes with a couple of lines of hairs close to and parallel to transverse carina. In *E. pulchella*, the premarginal line is so close to the transverse carina that there is only space for a couple of lines of hairs (coded ?).

51: Marginal area of T-1 of female, between dorsolateral convexities, (0) punctate; (1) smooth, except sometimes for rows of punctures parallel to submarginal line, producing premarginal band. In *Ancyla*, there is a smooth area behind the premarginal line, but the punctures extend beyond a premarginal band (coded 0). In *E. campestris* and *E. micheneri*, there are punctures behind the premarginal line, but they seem to belong to the premarginal band (coded 1).

52: Tomentum on marginal area of T-1 of female, between dorsolateral convexities, (0) absent; (1) present, extending to margin of tergum; (2) present, forming a premarginal band sometimes interrupted medially. *Eucerinoda* was coded 1, based on the description by Michener & Moure (1957:445), because hairs on metasoma of the specimen available to me were hard to see. In *E. fulvofasciata*, the limits of the premarginal band is disguised by the presence of a band of simple hairs that mixes with it and extends almost to the margin of the tergum (coded 2).

53: Tomentum on marginal area of T-2 of female (0) absent; (1) present, extending to margin of tergum; (2) present, forming complete band that does not extend to margin of tergum; (3) present, restricted to areas behind dorsolateral convexities. In *Ancyla*, the band originates near and extends beyond the margin of the tergum, suggesting a marginal band. A close examination shows that all hairs originate on the marginal area, not on the margin of the tergum (coded 3). In *E. fulvofasciata*, the band reaches the margin all the way across the tergum, except for a very narrow median area (coded 1).

54: Tomentum on marginal area of T-3 of female (0) absent; (1) present, extending to margin of tergum; (2) present, forming complete band that does not extend to margin of tergum; (3) present, restricted to areas behind dorsolateral convexities.

55: Tomentum on marginal area of T-4 of female (0) absent; (1) present, extending to margin of tergum; (2) present, forming complete band that does not extend to margin of tergum; (3) present, restricted to areas behind dorsolalteral convexities.

56: Apical hair fringes on T-1 to T-4 of female (0) absent; (1) present, sometimes interrupted medially, especially on T-1.

57: Transverse carina of T-1 of male (0) absent; (1) present.

58: T-7 of male (0) with distinct pygidial plate; (1) with no pygidial plate, apex of tergum bearing sharp transverse carina which is continuous with lateral carina; (2) pygidial plate absent, but suggested by apical carina with recurved margin; (3) pygidial plate and apical carina absent; lateral carina of tergum absent or inconspicuous. In *E. bicellularis* the carina is very poorly developed (coded 2).

59: S-6 of male (0) uniformly flat; (1) with median elevated area that broadens toward apex of sternum, forming carina or spine at each side; (2) depressed laterally with median longitudinal convexity. The form of S-6 is highly variable. Many taxa present autapomorphic states that were all coded as 0 as explained earlier. Some examples are the following: in *Tetrapedia* the sternum is concave; in *Ancyloscelis* there is a median longitudinal depression; in *Ptilothrix* there is a median longitudinal elevation; in *Paratetrapedia* there is a basal elevated area that extends medially, producing a sub-apical spine.

60: Disc of S-7 of male (0) subtriangular [Fig.8a]; (1) subquadrangular, with lateral edges arcuate, closest to each other medially [Fig.8b]; (2) pentagonal, latero-apical angles bearing a lateral process [Fig.8c]; (3) bilobed, lobes much broader than long [Fig.8d]; (4) bilobed, lobes much longer than broad [Figs.3,4,18,20 in Michener & Moure, 1957]; (5) trilobed [Fig.8e]; (6) subtriangular, with basilateral expansions [Fig.8f]; (7) reduced to narrow arc; (8) bilobed, lobes separated by membranous area [Fig.82 in Michener & Moure, 1957]; (9) broad, with two flat, triangular, latero-apical projections [Fig.8g]. Some characters on the disc of S-7 were clearly derived from others and this was incorporated in the matrix by means of two extra transformation series (mixed coding of Wiley *et al.*, 1991): 61 and 62:

61: Disc of S-7 of male subtriangular, with sclerotized line continuing apodemal submarginal line (0) in gentle continuous curve or in straight line; (1) distinctly produced laterally [Fig.8a, *la*]. Character 1 occurs only in some *Exomalopsis s.s.*

62: Disc of S-7 of male bilobed, much broader than long and (0) with posterior margin entire; (1) with small darkly sclerotized process on posterior margin [Fig.8d, *sp*]. Character 1 occurs only in some *Anthophorisca*.

63: Lateral processes of disc of S-7 of male (0) absent; (1) present [Fig.8h, *ld*]. These processes vary in length and shape.

64: Apical process of S-7 of male (0) absent or indistinguishable from the disc; (1) present as narrow transverse sclerite fused laterally to arms of disc [Fig.8b, *ap*]; (2) present as complex body which bears two free basilateral lobes under ventral surface of sternum [Fig.8h, *bl*].

65: Mid portion of basal edge of S-8 of male (0) pointed, basal edge forming two arcs with their concavities directed basad [Fig.9a,b]; (1) straight or broadly convex, whole edge producing a single arc [Fig.9c,d,e,f,g]. In *Ptilothrix*, the edge is barely pointed (coded 0).

66: Disc of S-8 (0) with no longitudinal carina or the carina short, near posterior margin [Fig.9b,c,e,f]; (1) with a longitudinal carina for all or almost all sternal length [Fig.9a,d]. In *Monoeca* the spiculum continues in a line across the disc, but this is not a carina such as in *Melissodes* or *Anthophorula* (coded 0). In *Chilimalopsis* and *Teratognatha* the carina is large, reaching half or a little more than half the length of the disc (coded 0).

67: Apical process of S-8 of male (0) subtriangular; (1) long, with single broad lobe separated from disc by very short constricted stalk [Fig.9a]; (2) long, bilobed, lobes separated by deep incision [Figs.2,5,11,14,17,19 in Michener & Moure, 1957]; (3) long, bilobed, lobes not separated by deep incision [Fig.9b]; (4) produced into two long, widely separated arms attached to single base [Fig.9c]; (5) long, with two dorsal sub-apical lobules and two flat subtriangular distal lobes [Fig.9d]; (6) long, with single bare, broad lobe separated from disc by strongly constricted stalk [Fig.9e]; (7) short, sometimes with two narrow projections [Fig.9f]; (8) broad, moderately long, with median apical incision [Fig.91 in Michener & Moure, 1957]; (9) long with single, broad, flat, hairy lobe, separated from disc by long strongly constricted stalk [Fig.9g]; (10) subtriangular, long, with two narrow apical projections [Fig.45 in Michener & Moure, 1957]. In *Xylocopa*, the process is very short, almost absent (coded 0). *Nomada* has a subtriangular process, which however is modified by a folded margin that bears setae and spines (coded 0).

68: Pockets on postero-lateral margin of disc of S-8 of male (0) absent; (1) present, bent dorsad [Fig.9c, *mp*]; (2) present, in same plane as disc [Fig.9a, *mp*]. In *Eucerinoda* and *Isomalopsis* there is a folding on the margin of the disc that may not be homologous to the more complex pockets in *Tarsalia* or *Teratognatha*. However, since it is in the same position it was coded (2).

69: Internal dorsal transverse ridge of gonocoxite (0) absent; (1) present [Fig.10, *dr*]. *Exomalopsis solitaria* does have a ridge, but it is oriented very differently (longitudinally) from that of other *Exomalopsis* (coded 1). In *E. tomentosa* the ridge is very short (coded 1).

70: Dorsal flange of gonocoxite (0) absent; (1) present [Figs.11a, 14 *df*]. In *E. trifasciata* it is reduced to little more than a carina (coded 1).

71: Lateral arms of gonocoxite (0) absent or short [Fig.12 *ag*]; (1) long [Fig.10, *ag*].

72: Gonocoxite (0) without ventrolateral sulcus; (1) with oblique ventrolateral sulcus [Fig.12, *vs*].

73: Ventral angle of gonocoxite: (0) simple; (1) produced into narrow lobe or spine [Fig.12, *sv*].

74: Internal wall of arm of gonocoxite, at apex, (0) simple; (1)

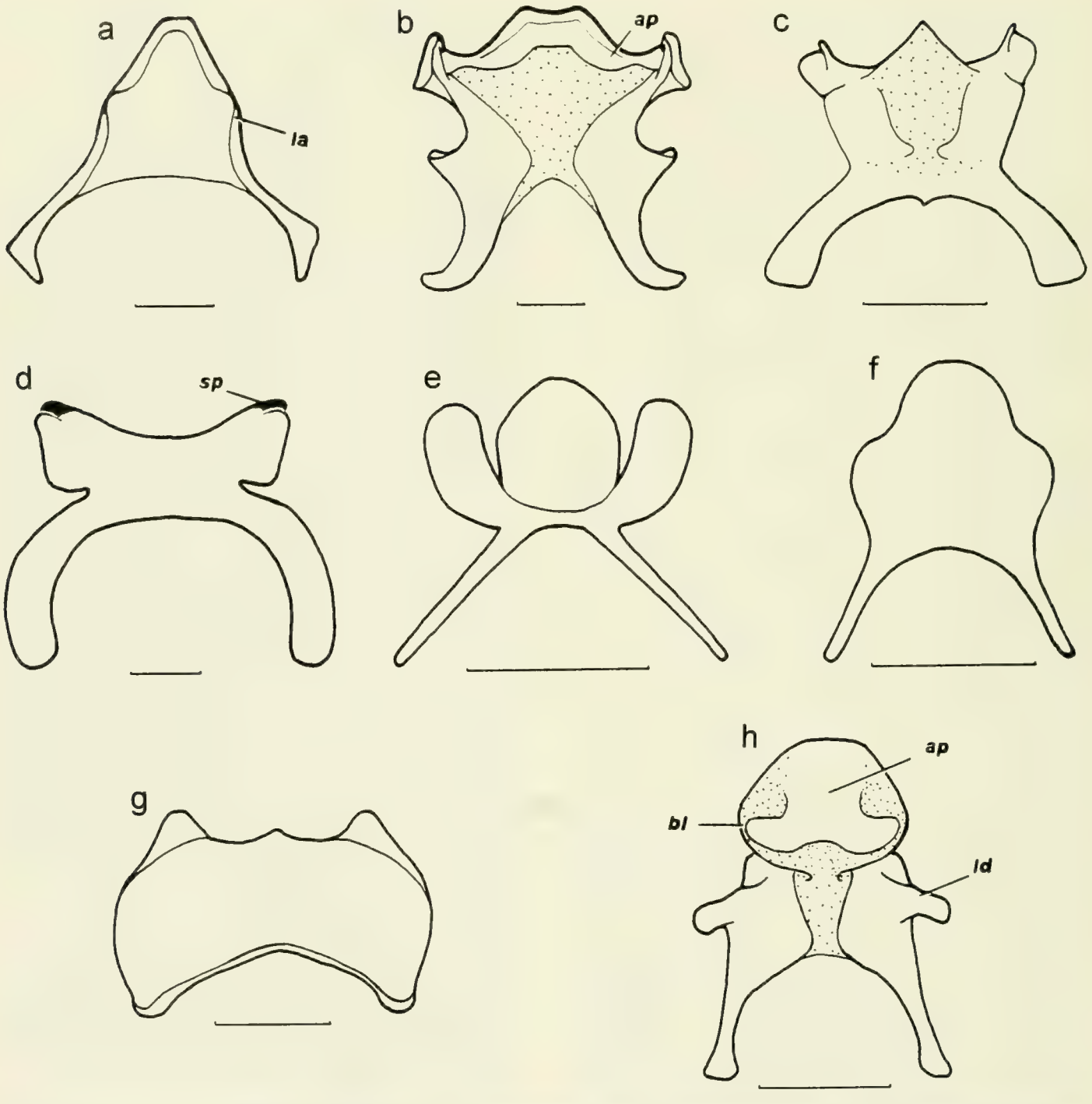


Fig. 8. Sternum 7 of (**a**) *E. (Exomalopsis) auroplosa*; (**b**) *E. (Phanomalopsis*) byersi*; (**c**) *Teratognatha modesta*; (**d**) *E. (Anthophorisca) micheneri*; (**e**) *Exomapis parvula*; (**f**) *Exomalopsis (Diomalopsis) bicellularis*; (**g**) *Isomalopsis niveata*; (**h**) *Exomalopsis (Phanomalopsis) jenseni*. *ap* = apical process of disc of S-7; *bl* = basolateral lobe of apical process; *la* = lateral production of sclerotized line of disc; *ld* = lateral process of disc; *sp* = sclerotized process of posterior margin. Hairs omitted. Stippled areas are nonsclerotized. Scale lines = 0.20 mm. * *Stilbomalopsis* in the classification proposed here.

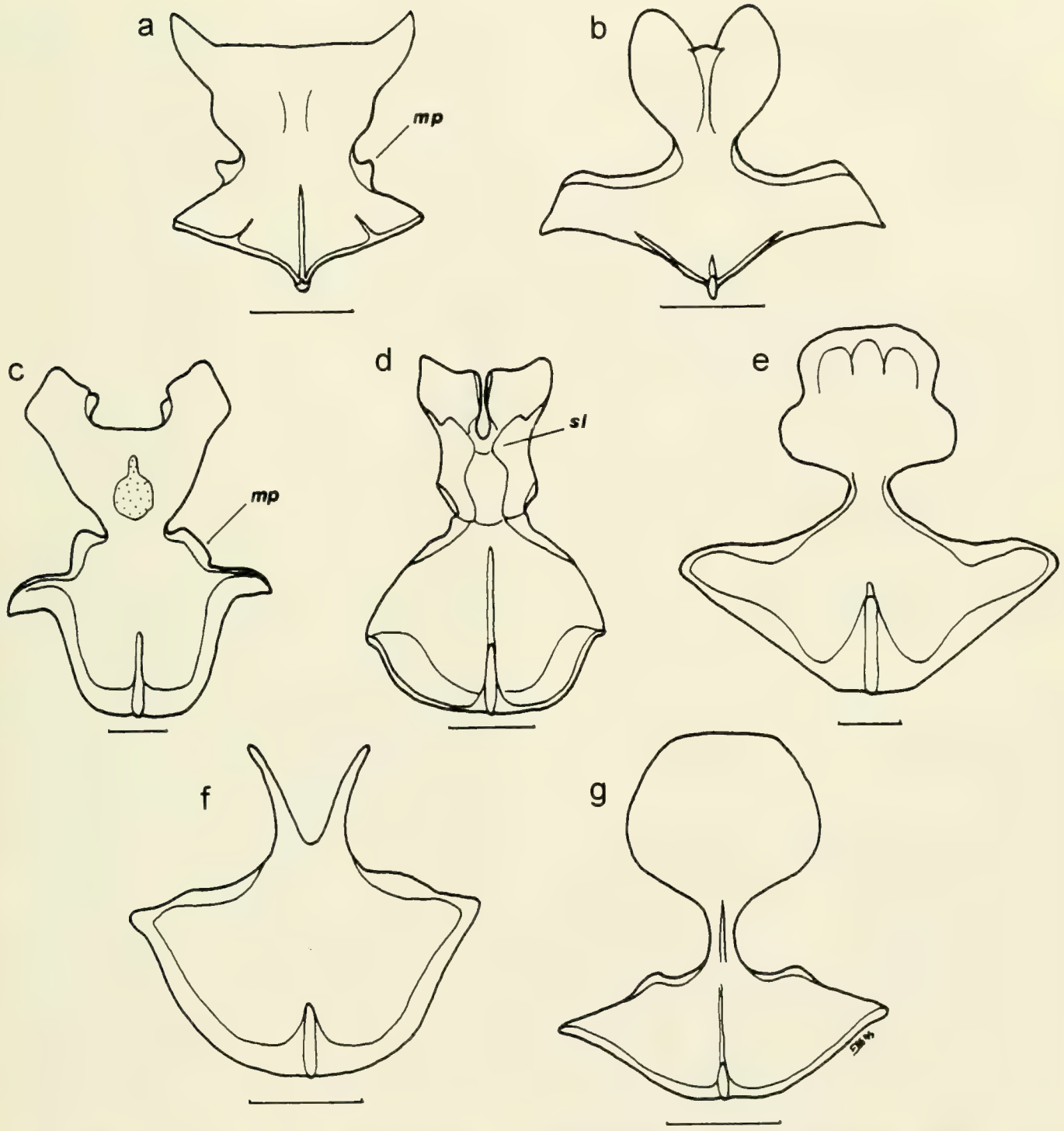


Fig. 9. Dorsal views of sternum 8 of (**a**) *Teratognatha modesta*; (**b**) *Ancyla oraniensis*; (**c**) *Exomalopsis (Phanomalopsis) jenseni*; (**d**) *Exomalopsis* (Anthophorisca) compactula*; (**e**) *Exomalopsis (Phanomalopsis) byersi*; (**f**) *E. (Exomalopsis) auropilosa*; (**g**) *Exomalopsis. (Diomalopsis) bicellularis*. *mp* = marginal pocket of disc; *sl* = subapical lobes. Stippled area is nonsclerotized. Hairs omitted. Scale lines = 0.20 mm. **Anthophorida* in the classification proposed here.

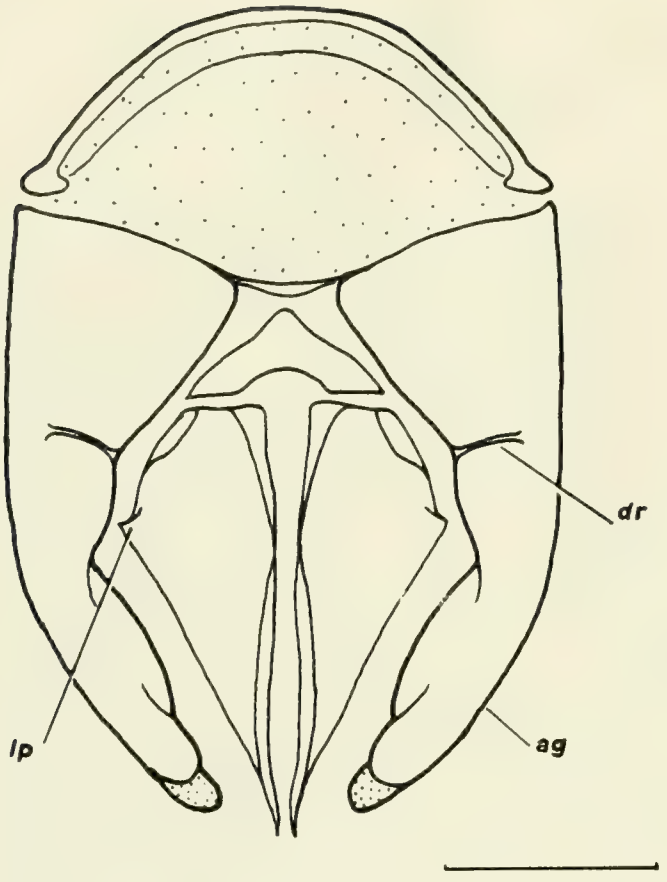


Fig. 10. Dorsal view of genitalia of *E. (Exomalopsis) auropilosa*. *ag* = arm of gonocoxite; *dr* = internal dorsal transverse ridge of gonocoxite; *lp* = lateral process of penis valve. Stippled areas are non-sclerotized. Scale line = 0.50 mm.

with narrow, dorsally directed process above gonostylus [Fig.12, *pw*]; (2) with narrow, horizontally or ventrally directed process below gonostylus [Fig.15 in Michener & Moure, 1957].

75: Peglike setae (0) absent; (1) present on subapical internal surface of gonocoxite [Fig.12, *pg*]; (2) present, on apex of gonocoxite [Fig.13b, *pg*].

76: Apex of gonocoxite (0) simple; (1) extended dorsally and ventrally, producing a median invagination that encloses base of gonostylus [Fig.14, *de,ve*]; (2) extended dorsally so that gonostylus originates subapically, beneath the extension.

77: Gonostylus (0) long, slender, sometimes with spherical apex [Figs.11,12]; (1) relatively long and slender, arising from apicolateral process of gonocoxite at pronounced angle [Fig.15]; (2) short, triangular in profile, broader at base than at apex [Fig.14]; (3) long, flattened dorso-ventrally, originating sub-apically under arm of gonocoxite [Fig.80 in Michener & Moure, 1957]; (4) broad, broader at apex than at base, flattened dorso-ventrally, originating at tip of gonocoxite [Fig.16]; (5) absent (perhaps modified into a broad lobe? See discussion below) [Fig.13a,b]. In *Nomada*, the gonostylus is somewhat compressed laterally, but was coded as (0).

78: Ventral surface of dorsal bridge of penis valves (0) simple; (1) with median process that overhangs laterally, supporting produced basal margin of penis valve [Fig.35 in Roig-Alsina & Michener, 1993].

79: Posterior margin of dorsal bridge of penis valves, medially (0) entire, notched or with small lobe; (1) expanded into a lobe that extends between (but not over) penis valves [Fig.11a, 17a]. In *Ctenoplectra*, the bridge is long and does extend between the penis valves, but the lobe is not produced mesally but overlaps the base of the penis valve (coded 0).

80: Base of penis valve, dorsally and behind dorsal bridge of penis valves, (0) sliding under or over dorsal bridge or touching it at a more or less perpendicular angle; (1) notched, producing a transverse plate which abuts dorsal bridge, both being on about same plane [Fig.13a, *tp*].

81: Outer side of penis valve (0) simple; (1) with lateral process [Figs.10,12 *lp*].

82: Dorsal blade of penis valve (0) absent; (1) present [Fig.13a,b *db*].

83: Ventral lobe of penis valve (0) absent; (1) present [Fig.11b *vl*].

84: Ventral surface of penis valve, subapically (0) evenly sclerotized in continuity with lateral surfaces of penis valve; (1) separated from lateral surfaces by mesal and external membranous sinuses [Fig.17b *ms,es*].

Analyses

Phylogenetic analyses were performed using the program Hennig86 version 1.5 (Farris, 1988 - provided by B. Alexander) in an IBM-compatible computer with a Cx486DLC processor. The matrix employed is shown in Table II. There, however, taxa are organized according to their relationships in the results, so that distribution of characters can be easily checked within and among clades.

To search for different islands of most parsimonious trees (Maddison, 1991), four sets of analyses were done. Before each one, the order of taxa in the matrix was changed by arbitraly rearranging the taxa. In each set of analyses, the command bb* was applied to trees that had been found by commands mhennig*, mhennig, hennig and hennig* (these commands are described in Farris,1988). Successive approximations weighting (Farris, 1969; 1988) was then applied to the results.

In the results and discussion below, focus will be given to the relationships among the main clades, not to the relationships among species. As in Silveira (1993), some strict consensus trees will be presented in which terminal taxa belonging to monophyletic groups were collapsed ("summaries of consensus trees"). These trees will appear to be fully resolved when polytomies were restricted to the relationships among taxa within the collapsed groups. Statistics shown for the cladograms are: length (l), consistency index (ci) and retention index (ri).

RESULTS

Cladograms

All sets of analyses produced minimum-length trees with the same statistics (l = 380; ci = 34 and ri = 72) and the same main features, as shown in the summary consensus tree in Fig.18. However, not all 16 analyses (four in each of the four sets defined above) yielded exactly the same trees: five of them yielded 66 trees, seven others yielded 63 trees, three yielded 61 and one yielded 127 trees. These trees differed only by the way in which the species of *Exomalopsis s.s.* + *Megomalopsis* were arranged. The consensus trees for the first five analyses were identical and showed *E. campestris* as the basal branch for the group, with *E. mellipes* and *E. fulvofasciata* as sister-species arising from a polytomy with the other eight species of *Exomalopsis s.s.* (Fig.19a). The nine following analyses (yielding 63 and 61 trees) yielded another set of identical consensus trees (Fig.19b). In these, *Exomalopsis campestris* is the sister species of *E. mellipes*, and they arise from an unresolved clade including *E. vernoniae, E. analis, E. to-*

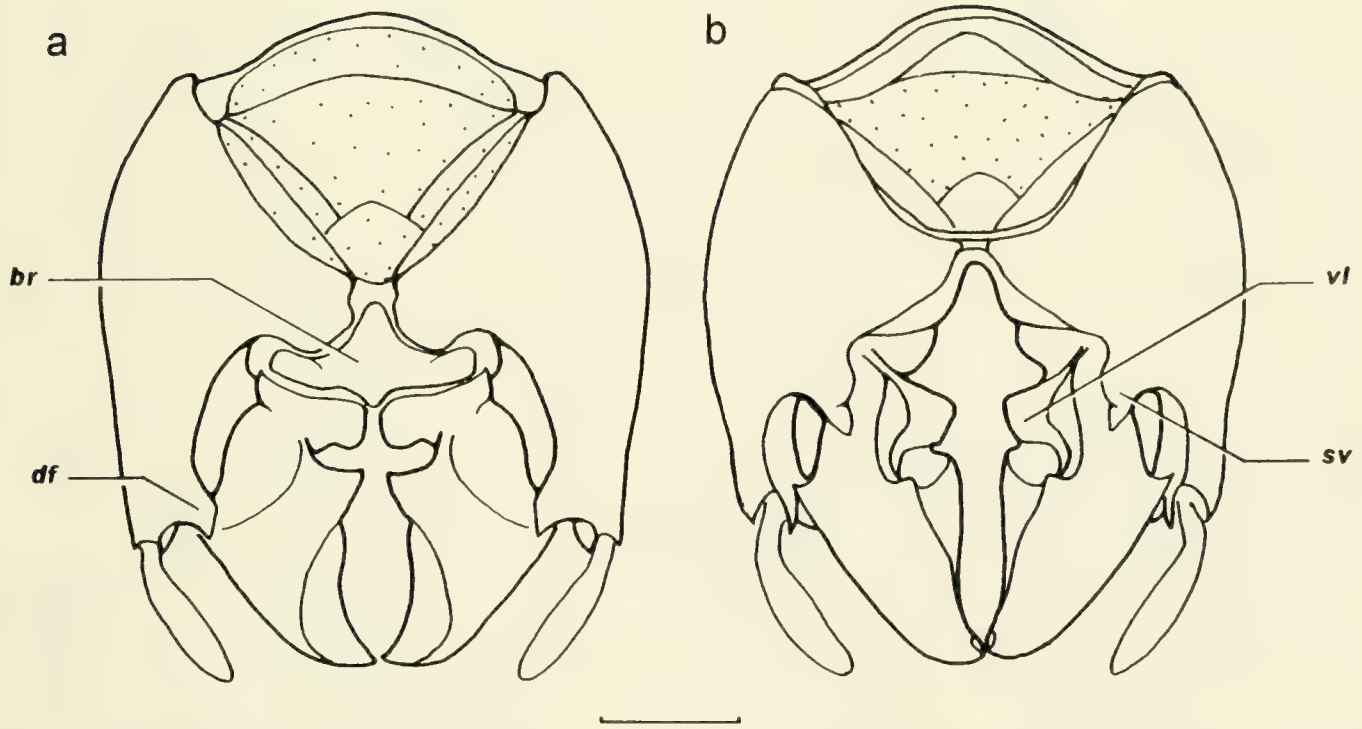


Fig. 11. Genitalia of *Exomalopsis (Phanomalopsis*) solani*. (**a**) dorsal view; (**b**) ventral view. *br* = dorsal bridge of penis valves; *df* = dorsal flange of gonocoxite; *sv* = spine of ventral lobe of gonocoxite; *vl* = ventral lobe of penis valve. Scale line = 0.30 mm. * *Stilbomalopsis* in the classification proposed here.

mentosa, E. pulchella, E. fulvofasciata and *E. bruesi*. They all arise from a polytomy that also includes *E. auropilosa, E. similis* and *E. mourei*. The consensus tree for the analysis yielding 127 trees (Fig.19c) shows all species of *Exomalopsis s.s.* + *Megomalopsis* arising from a single polytomy.

Successive approximations weighting for each of the 16 analyses produced different numbers of equally parsimonious trees with different statistics, depending on the number of initial trees. Some representative numbers are: l = 824, ci = 65, ri = 89, 1736 trees; l = 811, ci = 63, ri = 88, 984 trees; l = 818, ci = 66, ri = 89, 298 trees. The consensus trees obtained after successive approximations, however, were the same for all analyses. A summary of them is reproduced in Fig.20. The main clades obtained before and after successive approximations are the same. After successive approximations, *Diomalopsis* is always the sister-group to *Exomalopsis s.s.* + *Megomalopsis*. When characters are given equal weight, *Diomalopsis* sometimes appears as the sister group to the *Exomalopsis solani* species-group. The characters supporting each group and the alternative relationships among them are presented and discussed below.

The following account is restricted almost entirely to the unique synapomorphies supporting the main clades. A few homoplastic characters are cited when there were reasons to suspect that they are only superficially similar to features appearing elsewhere in the cladograms, or when they are constant within the clade being discussed and not frequent outside it. The distribution of the characters can be

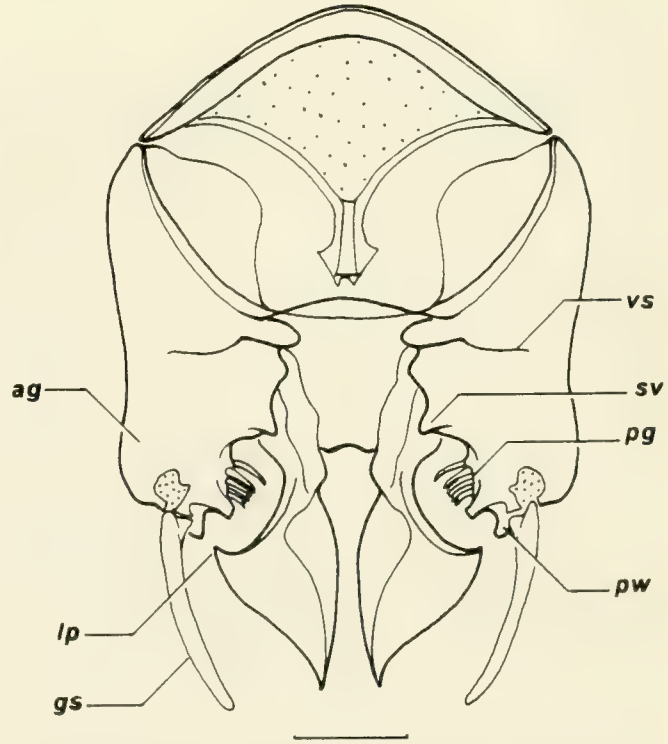


Fig. 12. Ventral view of genitalia of *Ancyla oraniensis*. *ag* = arm of gonocoxite; *gs* = gonostylus; *lp* = lateral process of penis valve; *pg* = peglike setae; *pw* = process of internal wall of gonocoxite; *sv* = spine of ventral lobe of gonocoxite; *vs* = ventrolateral sulcus of gonocoxite. Stippled areas are nonsclerotized. Scale line = 0.30 mm.

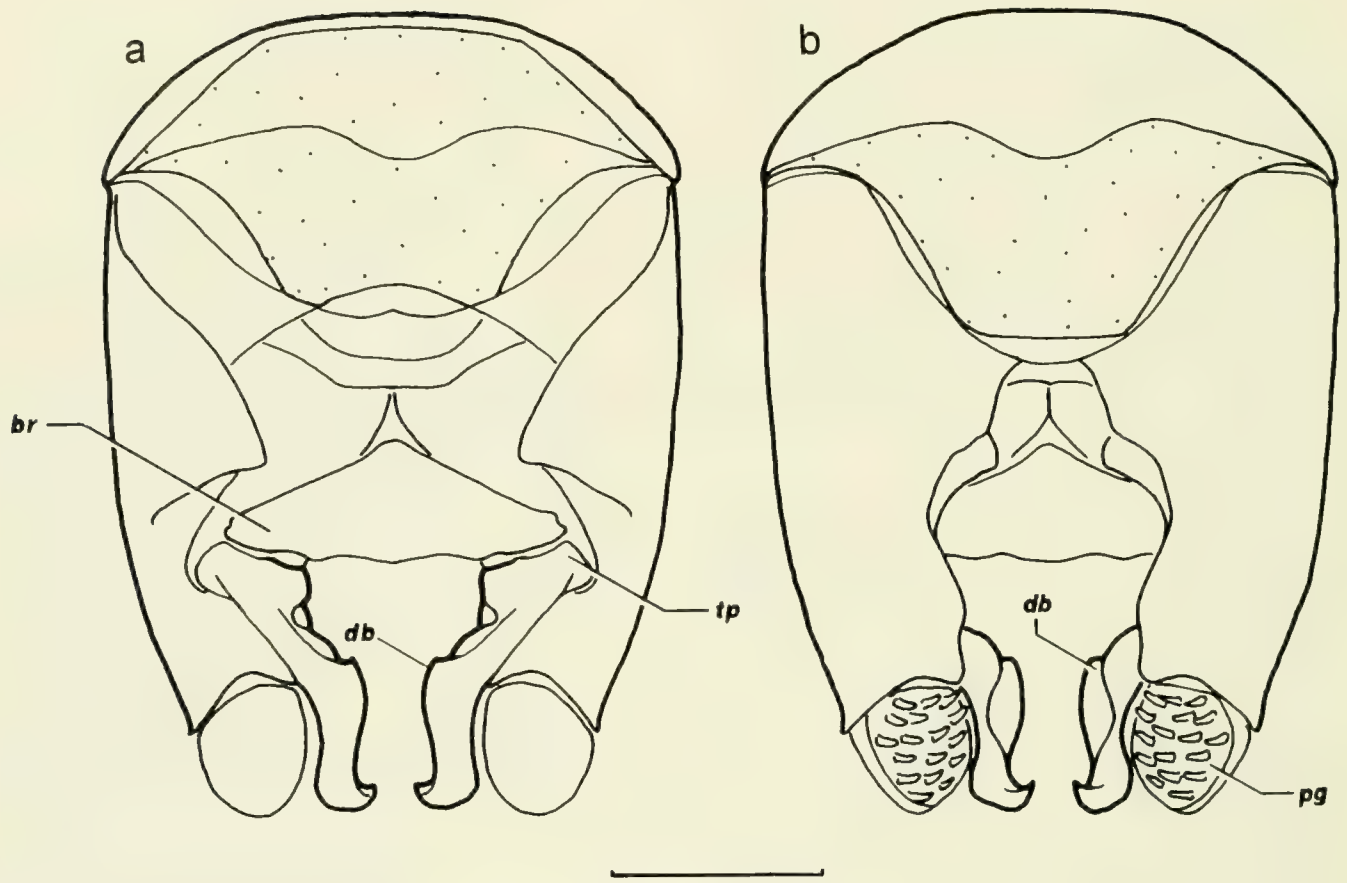


Fig. 13. Genitalia of *Exomalopsis* (Anthophorisca) texana*. (**a**) dorsal view; (**b**) ventral view. *br* = dorsal bridge of penis valves; *db* = dorsal blade of penis valve; *pg* = peglike setae; *tp* = transverse plate of base of penis valve. Stippled areas are nonsclerotized. Scale line = 0.25 mm. * *Anthophorula* in the classification proposed here.

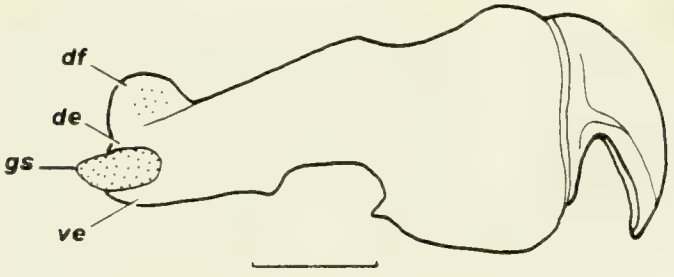


Fig. 14. Outer lateral view of genitalia of *E. (Exomalopsis) campestris* (penis valves ommited, gonobase at right). *de* = dorsal extension of gonocoxite; *df* = dorsal flange of gonocoxite; *gs* = gonostylus; *ve* = ventral expansion of gonocoxite. Stippled areas represent nonsclerotized areas in the specimen. Scale line = 0.50 mm.

checked in the trees in Figs. 21, 22 and 23, which were selected, among the many trees obtained in the several analyses, to represent alternative hypotheses for the relationships among the main lineages of Exomalopsini. The tree represented in Fig.23 was obtained after successive approximations weighting.

Phylogenetic Relationships among the Outgroups

Conclusions about the relationships among the outgroup taxa based on the present analyses should not be overemphasized. This is because few representatives of each lineage were employed and characters were not intensively surveyed among them. It is noteworthy, however, that the relationships among the outgroups were stable throughout the analyses (Figs.18,20-23). Xylocopinae (represented by *Manuelia* and *Xylocopa*) and Nomadinae (represented by *Nomada*) were the first two groups to branch off, followed by Tetrapediini, and the eucerine line (as defined by Silveira, 1993)

An interesting group is the clade including the Ancylini, Eucerini and Exomalopsini (*sensu* Roig-Alsina & Michener, 1993). The only unique character common to all members of this clade is the penicillus on the hind basitarsus of females (character 41-2). The shape of the apical process of sternum VIII of male (character 67-1; Fig.9a), which is hypothesized to be the ancestral synapomorphic condition for this clade, is actually present only in *Teratognatha* + *Chilimalopsis* and in *Eremapis*. All other lineages are characterized by alternative shapes.

This clade is divided in two broad lineages: one is com-

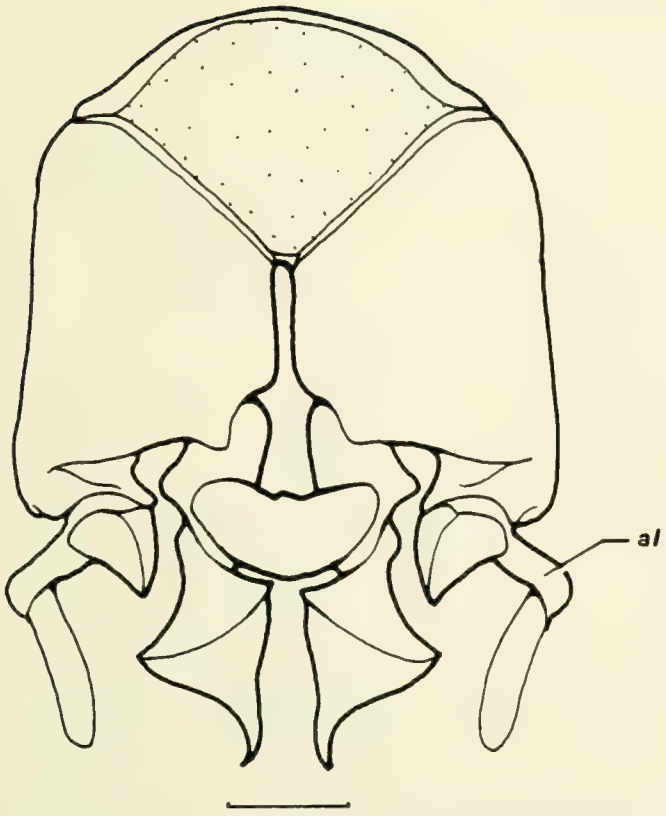


Fig. 15. Dorsal view of genitalia of *Chilimalopsis* sp. *al* = apicolateral process of gonocoxite. Stippled areas represent nonsclerotized areas in the specimen. Scale line = 0.10 mm.

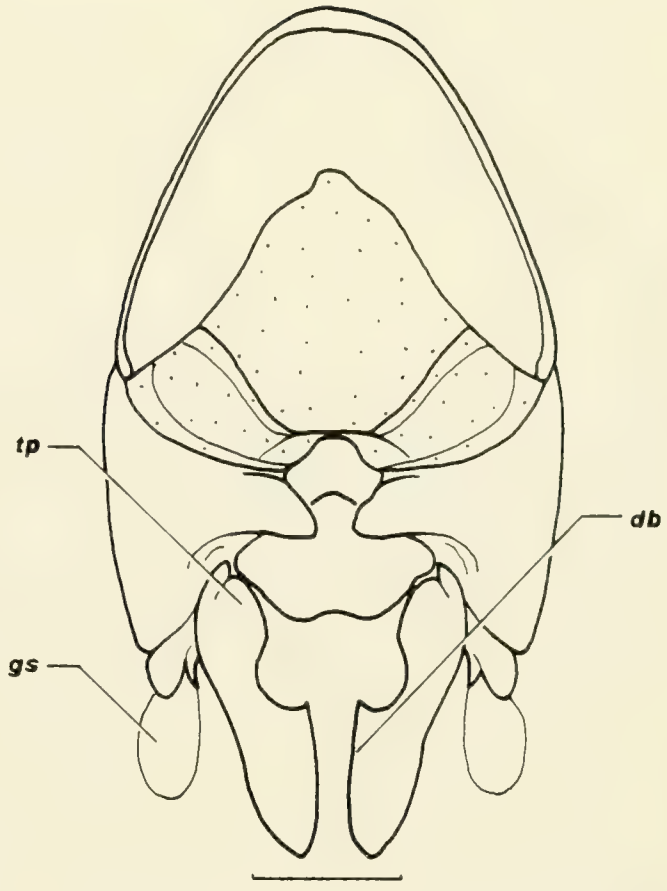


Fig. 16. Dorsal view of genitalia of *Exomalopsis* (Anthophorula) completa*. *db* = dorsal blade of penis valve; *gs* = gonostylus; *tp* = transverse plate of base of penis valve. Stippled areas represent nonsclerotized areas in the specimen. Scale line = 0.20 mm. * *Anthophorula* in the classification proposed here.

prised of the Ancylini, the Eucerini and *Teratognatha* + *Chilimalopsis*; the other by Exomalopsini minus *Teratognatha* + *Chilimalopsis*. The first lineage is supported by a unique synapomorphy, the peglike setae on the subapical internal surface of the gonocoxite (character 75-1; Fig.12, *pg*). These setae, however, are known to be present in other bees not included in the present analyses (Roig-Alsina & Michener, 1993). Other homoplastic characters supporting this clade are: the expansion of the trunk of the anterior tibial spur (character 43-1; Fig.7b) and the process of the internal wall of the arm of the gonocoxite (character 74-1; Fig.12, *pw*). The expansion of the anterior tibial spur has similar structure in *Ctenoplectra*. *Ctenoplectra* and *Exomalopsis aureosericea* also possess similar processes on the arm of the gonocoxite. In trees obtained after successive approximations, the narrow pterostigma (character 35-1; Fig.6a) also appears as a synapomorphy for this clade. This also is a feature of the Emphorini and of *Anthophorula*. The monophyly of Ancylini is supported by two features: the ventrolateral sulcus of the gonocoxite (character 72-1; Fig.12, *vs*), which was already pointed out by Silveira (1993), and a median longitudinal convexity in sternum VI of male (character 59-2). Another character supporting Ancylini is the long, bilobed apical process of sternum VIII, whose lobes are not separated by a long incision (character 67-3; Fig.9b). This character appears also in *Ptilothrix*. In the Ancylini, the lobes are separated by a short but wide incision, and the median longitudinal line between them is developed dorsally as a bare ridge that continues through the long basal stalk. In *Ptilothrix* the two lobes are separated apically by a narrow incision between two denticles. The median longitudinal line between the lobes is more heavily sclerotized than the rest of their surfaces (but does not constitute a ridge) and is covered by hairs. This median line does not reach the basal stalk, which is also much shorter than in Ancylini.

Under the present phylogenetic hypothesis, the genera *Teratognatha* and *Chilimalopsis* are combined in a clade that is the sister-group of the Eucerini. No unique feature supports this group and the only character supporting this clade in all trees examined is the disc of female T-1, which is longer than the marginal area (character 49-0). This character is also present in *Eremapis*, in the *Exomalopsis solani* species-group and in *Exomalopsis jenseni*. Eucerini and *Teratognatha* + *Chilimalopsis* are not very similar and the weak support their sister-group relationship receives sug-

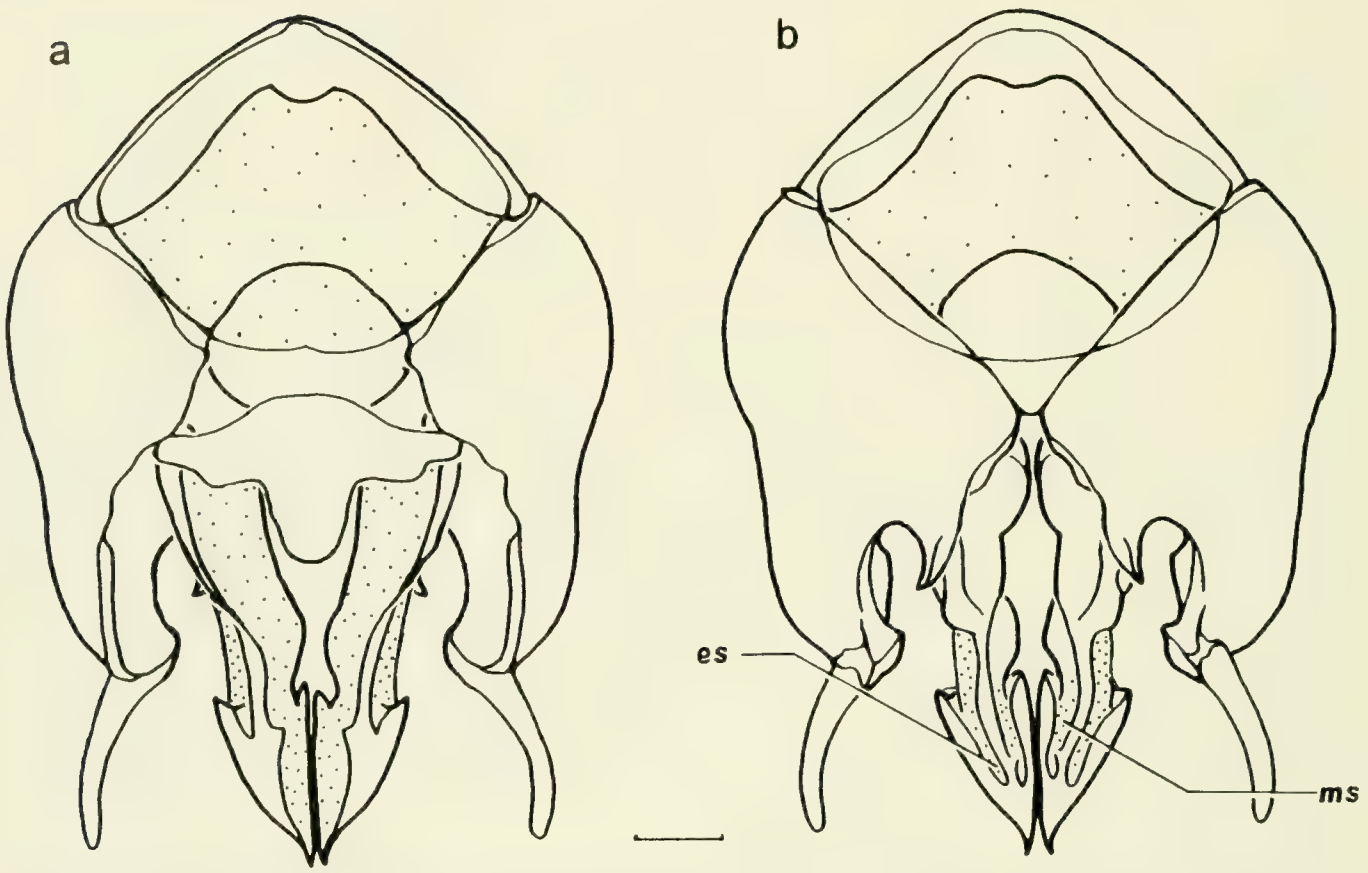


Fig. 17. *Exomalopsis (Phanomalopsis) jenseni* (male): (**a**) dorsal and (**b**) ventral views of genitalia; *ms* = mesal sinus of penis valve; *es* = external sinus of penis valve. Scale line = 0.20 mm.

gests that one should not put much confidence in this hypothesis.

The clade composed by *Teratognatha* and *Chilimalopsis* is supported by three unique synapomorphies: the ill-developed scopa composed of minutely and sparsely branched hairs (character 40-3), the pentagonal disc of S-7 of male (character 60-2; Fig.8c) and a relatively long and slender gonostylus, which arises from the apicolateral process of the gonocoxite at a pronounced angle (character 77-1; Fig.15). An interesting homoplastic character supporting this clade is the pockets of the posterolateral margin of the disc of S-8 of the male (character 68-2; Fig.9a, *mp*). This character is also present in *Eucerinoda* and *Isomalopsis*, but in those genera the pockets do not protrude out of the margin of the sternum, as they do in *Teratognatha* and *Chilimalopsis*. The results show *Chilimalopsis* as a paraphyletic assemblage in relation to *Teratognatha*.

The relationships of *Teratognatha* and *Chilimalopsis*, as described above, make Exomalopsini (as defined by Roig-Alsina & Michener, 1993) polyphyletic. Exomalopsini, thus, should be limited to the genera *Eremapis, Isomalopsis* and *Exomalopsis* (*sensu* Michener & Moure,1957). A single unique synapomorphy supports the tribe under this definition: a glabrous, median, longitudinal line delimited by two rows of hairs on the labrum of females (character 6-2; Fig.2a). Other characters supporting this clade are: the obliquely truncate apex of the marginal cell (character 34-2; Fig.6a,b) and the long pterostigma (character 36-0; Fig.6b—reduced in *Anthophorula s.s.*). Character 34-2 is present also in *Ancyloscelis, Teratognatha modesta* and *Chilimalopsis impressifrons*. Character 36-0 is present in Tapinotaspini, and in many groups outside the eucerine line.

Phylogenetic Relationships within Exomalopsini

Eremapis appears as the basal lineage of Exomalopsini (as defined above) both when characters are equally weighted and after successive approximations. Six other main lineages are defined in both analyses: *Anthophorula* + *Isomalopsis, Anthophorisca*, the *Exomalopsis solani* species-group of *Phanomalopsis, Phanomalopsis* (excluding *E. solani* and related species), *Diomalopsis* and *Exomalopsis s.stricto* + *Megomalopsis*. These lineages share three unique features: the paraocular cilia (character 14-1); the dense tomentum on the ventral surface of the frontal coxa of females (character 38-1) and the short apical process of S-8, which sometimes bears two narrow projections (character 67-7; Fig.9f). The paraocular cilia are a unique feature among bees and are present in

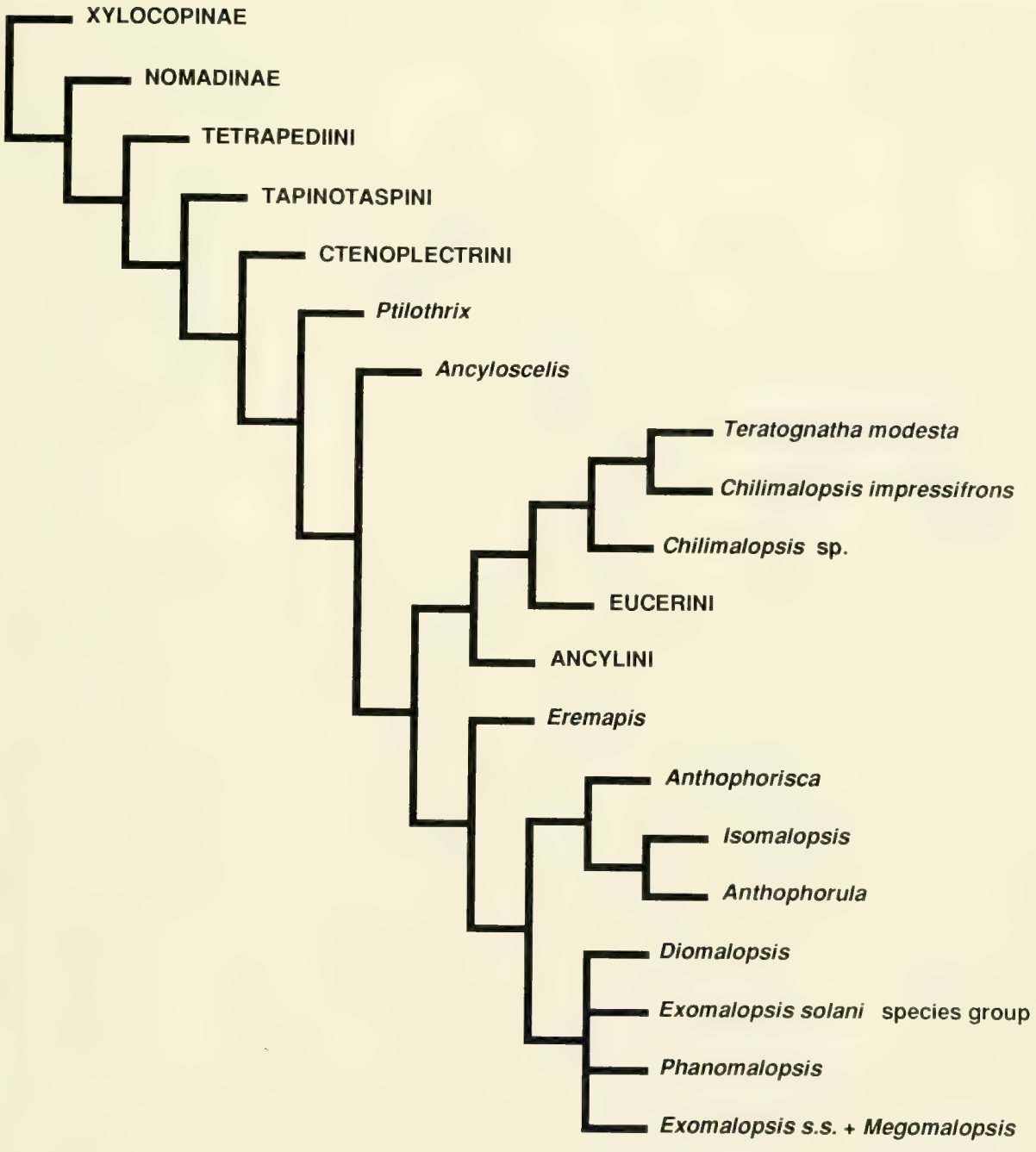


Fig. 18. Summary of the consensus tree for 1081 trees (l = 379; ci = 34; ri = 72) resulting from the analyses with equally weighted characters. *Exomalopsis solani* and the other species in its group were hitherto considered to be in the subgenus *Phanomalopsis*.

all examined species of *Exomalospis* (*sensu* Michener & Moure, 1957). The pilosity on the front coxae of the females is also very distinctive. In *Anthophorisca* it is changed from dense tomentum to decumbent minute simple hairs. The apical process of S-8 of the male also varies among three groups within this lineage: *Phanomalopsis*, *Exomalopsis solani* species-group and *Diomalopsis*.

In anticipation of the taxonomical changes proposed below, *Exomalopsis s.s.* + *Megomalopsis* and the *Exomalopsis solani* species group will be referred to henceforth as *Exomalopsis s.s.* and *Stilbomalopsis*, respectively.

No unique synapomorphy supports *Anthophorula*+*Isomalopsis*. Homoplastic characters supporting this clade are the expansion of the trunk of the anterior tibial spur, which ends in a strong angle (character 43-2; Fig.7c) and the transverse carina on T-1 of males (character 57-1). Character 43-2 is

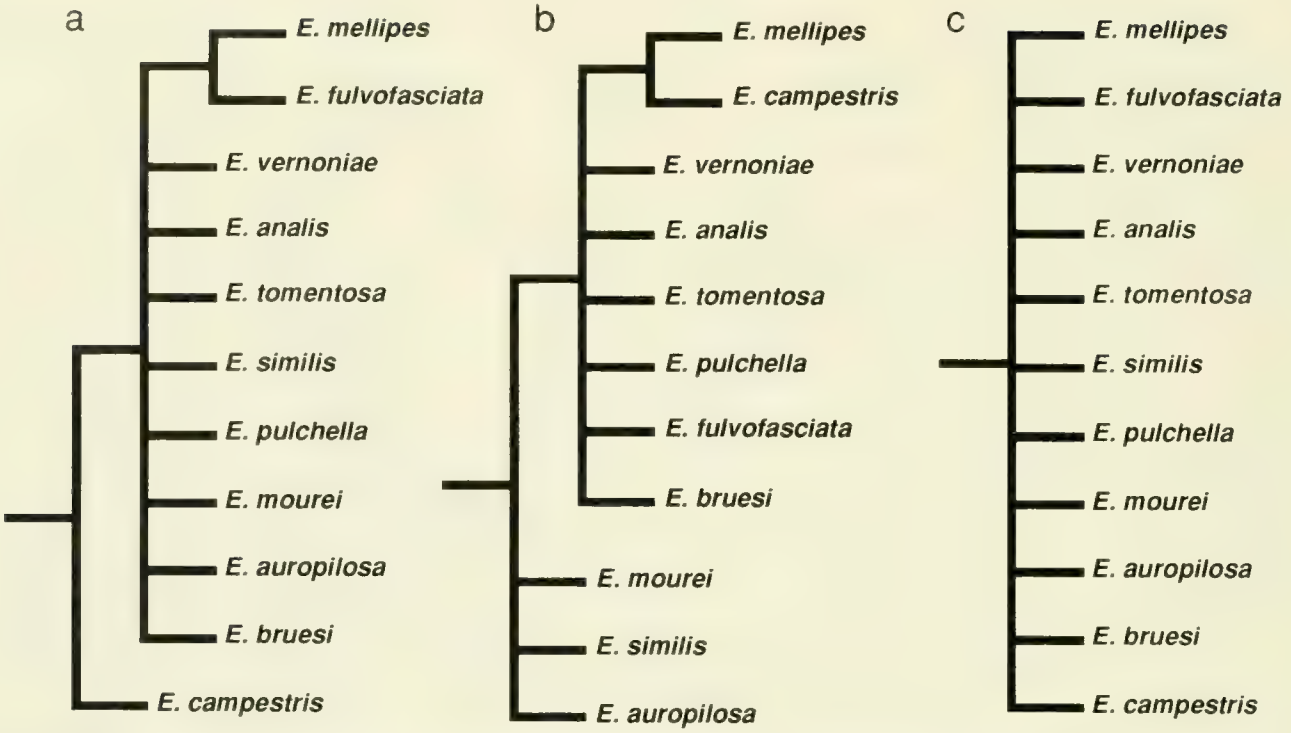


Fig. 19. Different topologies (**a**, **b** and **c**) within the branch shown as *Exomalopsis* s.s. (including *Megomalopsis*) in the consensus tree in Fig.18. Each of the different topologies is the outcome of one or more of the 16 analyses performed with equally weighted characters.

unique within the Exomalopsini, but also occurs in Tapinotaspini; character 57-1 appears also in *Exomalopsis jenseni*.

Some of the homoplastic features supporting the monophyly of *Anthophorula s.s.* are the reduced stigma (characters 35-1 and 36-1; Fig.6a) and the presence of a distinct pygidial plate in the males (character 58-0). These are unique features among the Exomalopsini which, however, occur elsewhere among the outgroups. Although no unique character was found to be present in all *Anthophorula s.s.* there are two unique synapomorphies for all *Anthophorula s.s.*, except *A. euphorbiae*. Since this is a minute species, the absence of these features may be consequence of size reduction. The putative synapomorphies shared by the other *Anthophorula s.s.* are: the marginal area of T-1 of female, which is depressed in relation to the disc (character 48-1) and the structure of the apical process of S-8 of males, which possesses two dorsal sub-apical lobes and two flat, subtriangular distal lobes (character 67-5).

Anthophorisca is supported by two unique synapomorphies. One is the presence of the short, fine, decumbent hairs on the ventral surface of the front coxae of females (character 38-2), which is a modification of the tomentum that covers this surface in all other Exomalopsini (as defined above), except *Eremapis*. The other unique synapomorphy is the presence of peglike setae on the internal surface of the apex of the gonocoxite. Another character supporting the monophyly of this group deserves some discussion. I originally interpreted the lobe at the apex of the gonocoxa of *Anthophorisca*, not as the gonostylus, but as the parapenial lobe (Roig-Alsina & Michener, 1993), and I coded the gonostylus as absent (character 77-5; Fig.13a,b). My interpretation was based on the presence of the peglike setae, which I considered to be homologous with those present in Ancylini, Eucerini and *Teratognatha* + *Chilimalopsis*. The tree topologies obtained in the parsimony analyses, however, suggest that the peglike setae are *de novo* acquisitions of *Anthophorisca*. If this is the case, the lobe at the apex of the gonocoxa in this group may be a unique transformation of the gonostylus and thus an additional strong support for its monophyly. If the first hypothesis is correct, the absence of a gonostylus would probably be a good synapomorphy for the group, since the only other taxon included in this study that lacks a gonostylus is *Xylocopa*.

In the cladograms, the monophyly of *Anthophorula*+*Isomalopsis*+*Anthophorisca* is supported by a unique synapomorphy: the shape of the disc of S-7 of male, which is bilobed with the lobes broader than long (character 60-3; Fig.8d). This is changed in *Isomalopsis* to a broader structure with two apicolateral, flat, triangular projections (character 60-9; Fig.8g). An alternative interpretation of the homologies between these two arrangements would be to consider the broad structure in *Isomalopsis* as an enlargement of the apodemes and the triangular projections as reduced lobes. Additional support for this clade would be the transverse basal plate and the dorsal blade of the penis valves (characters 80-1 and 82-1; Figs.13a, *tp* and 13a,b, *db*). These characters would have been lost by *Isomalopsis*. Additional steps are not required in the cladograms for the accep-

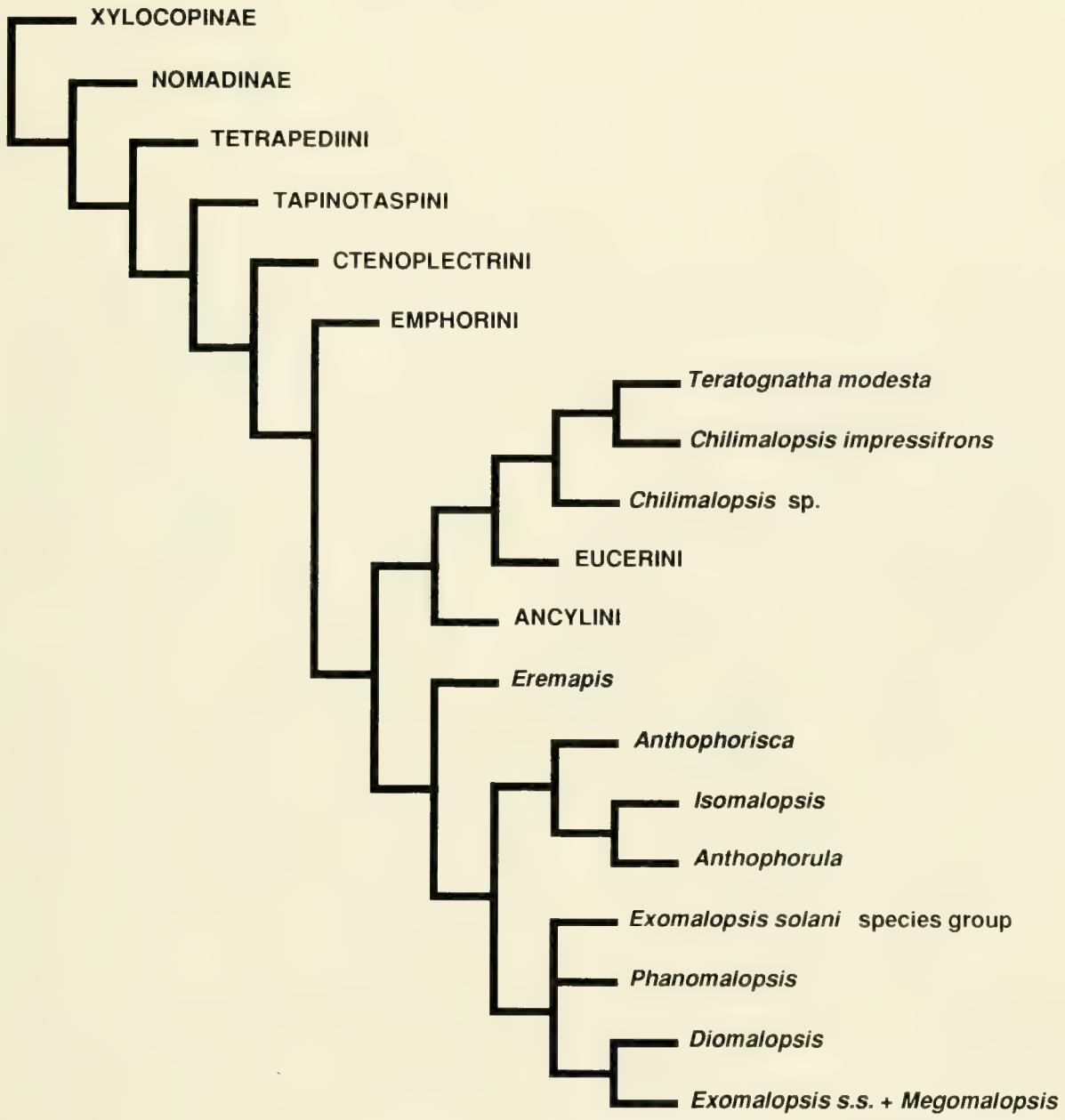


Fig. 20. Summary of the consensus trees for all analyses after successive approximations weighting. Different analyses produced different numbers of trees with slightly different statistics, but all resulted in this same consensus tree.

tance of this last hypothesis.

The analyses presented here indicate that the subgenus *Phanomalopsis*, as defined by Michener & Moure (1957), is not a monophyletic assemblage, but instead contains two independent lineages. One, *Phanomalopsis s.s.*, is composed mainly of South American species and contains the type species of the subgenus, *E. jenseni*. The other lineage, *Stilbomalopsis*, is a very distinctive group of species (*E. solani* being the most common) which is mostly restricted to the semi-desertic areas of Mexico and the southwestern United States.

A single unique synapomorphy supports the monophyly of *Phanomalopsis s.s.*: the complex (but variously modified) apical process of S-7 of the male, which bears two free basilateral lobes under its ventral surface (character 64-2; Fig.8h, *bl*). One of the homoplastic characters supporting this clade is the two long, widely separated arms of the apical process of S-8 of males (character 67-4; Fig.9c). This character may indeed be a good synapomorphy for this clade. It appears again only in *Anthophorula euphorbiae*. In this species it is not so developed and may be the result of the simplification of the specialized process of other species of *Anthophorula s.s.* It should be mentioned, on the other hand, that in *Exoma-*

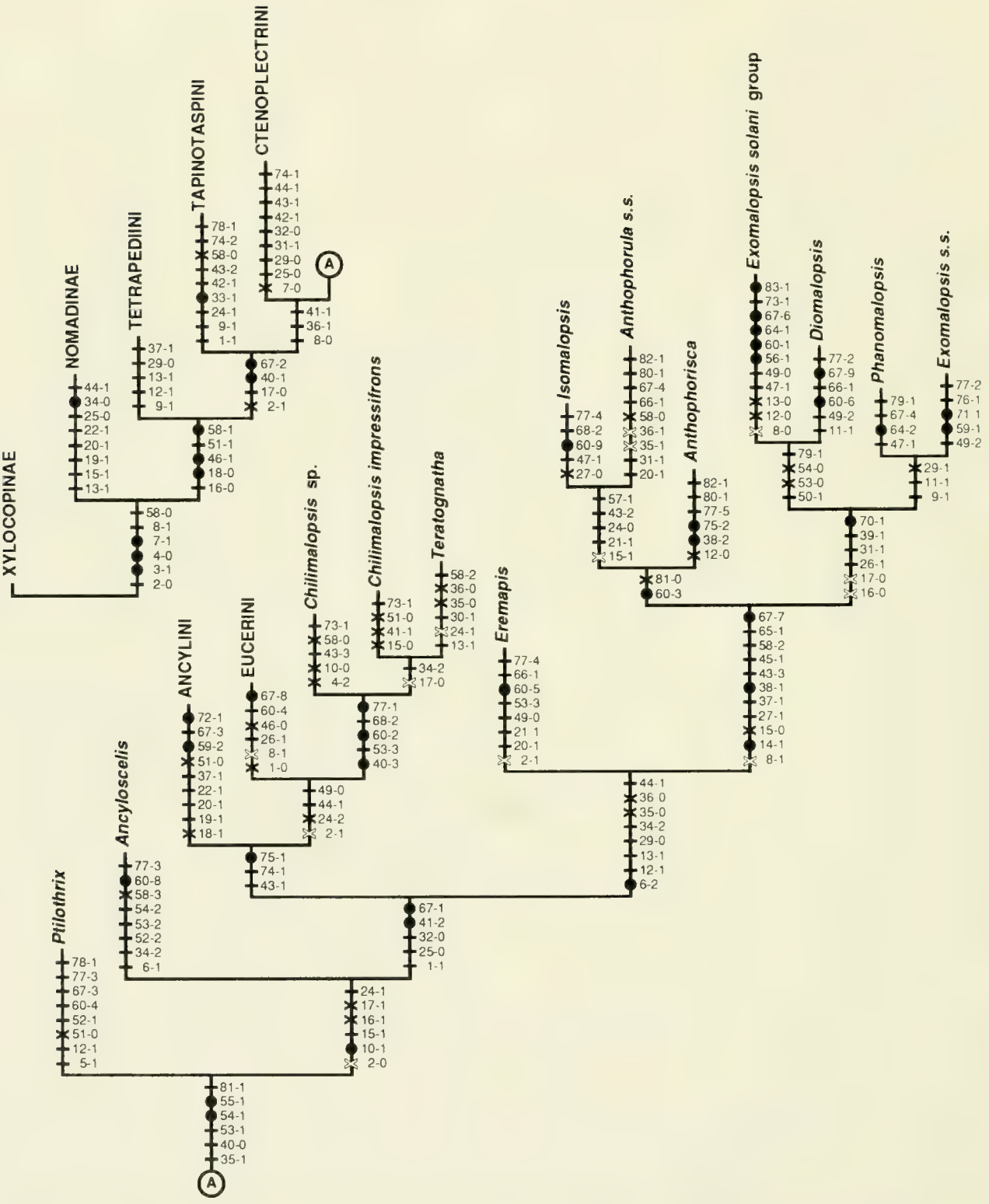


Fig. 21. Phylogenetic relationships of Exomalopsini. Example in which *Diomalopsis* is the sister-group of the *Exomalopsis solani* species group (= *Stilbomalopsis* in the classification proposed here), and *Phanomalopsis* is the sister-group of *Exomalopsis* s.s. (including *Megomalopsis*) (l = 380; ci = 34; ri = 72). Bars indicate changes that occur independently elsewhere in the tree; black crosses indicate reversals; white crosses indicate re-reversals and dots indicate changes occurring only once on the tree. The base of the tree is at the upper left.

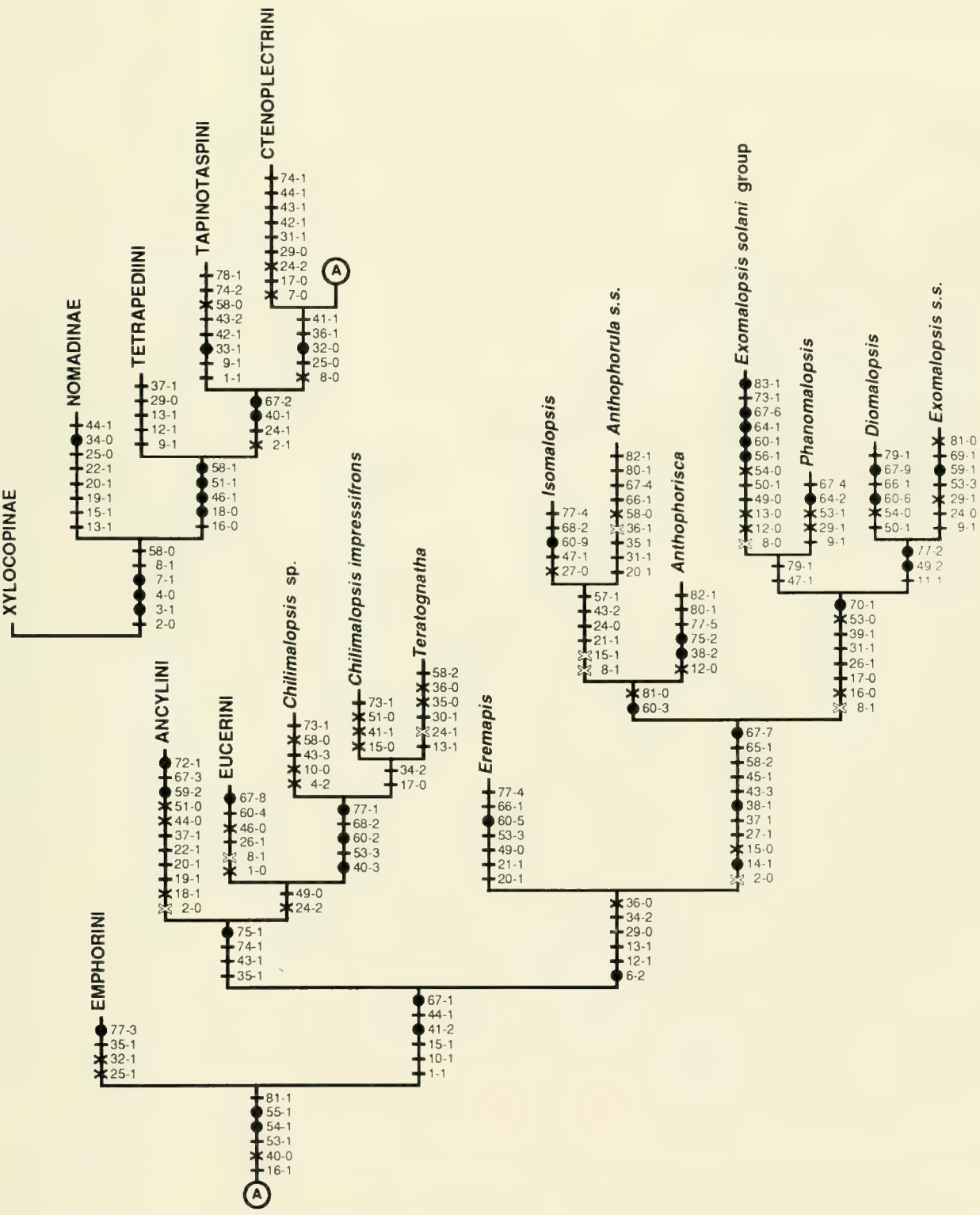


Fig. 22. Phylogenetic relationships of Exomalopsini. Example in which *Diomalopsis* is the sister-group of *Exomalopsis* s.s., and *Phanomalopsis* is sister to the *Exomalopsis solani* species group (= *Stilbomalopsis* in the classification proposed here) and *Diomalopsis* + *Exomalopsis* s.s. (including *Megomalopsis*) (l= 380; ci = 34; ri = 72). Symbols as in Figure 21. The base of the tree is at the upper left.

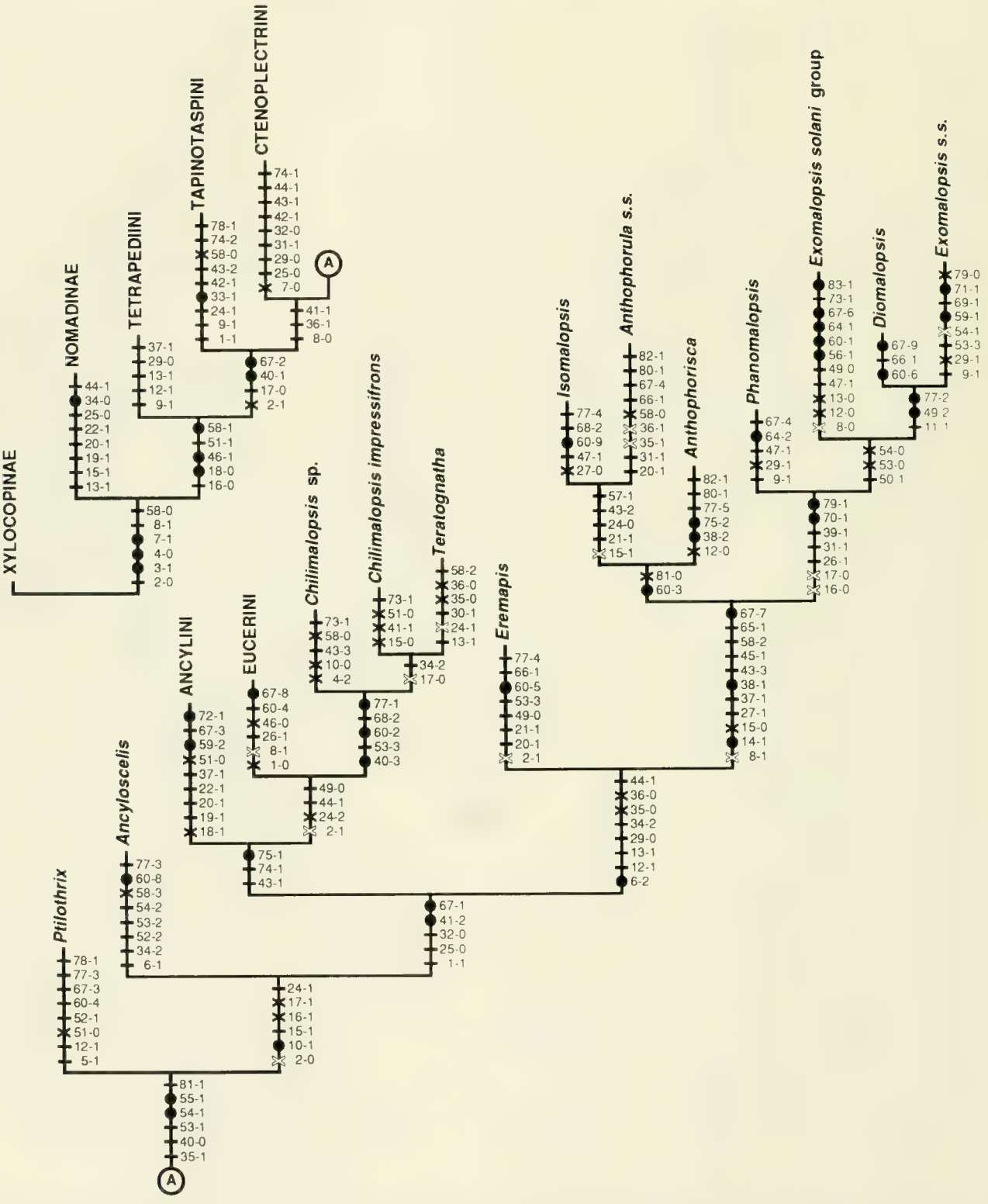


Fig. 23. Phylogenetic relationships of Exomalopsini. Example in which *Diomalopsis* is the sister-group of *Exomalopsis* s.s. (including *Megomalopsis*) and *Phanomalopsis* is sister to the *Exomalopsis solani* species group (= *Stilbomalopsis* in the classification proposed here). One of 1736 trees obtained after successive approximations weighting (l = 824; ci = 65; ri = 89). Symbols as in Figure 21. The base of the tree is at the upper left.

Table II. Data matrix employed in the phylogenetic analyses. Numbers in italics are the character numbers as given in the text.

		1	*2*	*3*	*4*	*5*	*6*	*7*	*8*
	123456789	*0123456789*	*0123456789*	*0123456789*	*0123456789*	*0123456789*	*0123456789*	*0123456789*	*01234*
Manuelia	110200000	0000001110	0000110001	0010100000	0100000000	0000000030	0000010000	0000000000	00000
Xylocopa	0102?0000	0000001111	0000210001	0010111090	200000?00?	0000000030	7000000000	0000000500	00000
Nomada	001000110	0001011111	1010200001	0010000000	?000100000	0000000000	0000000000	0000000000	00000
Tetrapedia	001000111	0011000100	0000210000	0010100100	2000001001	0100000010	0000000000	0000000000	00000
Paratetrapedia	110000111	0000011100	1000110001	0011100000	1012001001	00?0000030	4000000200	0000200010	01000
Monoeca	111000111	0010000000	0000110001	0011100000	1012001001	1100000000	0000010?00	0000200010	00000
Ctenoplectra	011000000	0000000000	0000200000	0100101000	1111101001	0100000010	0000000200	0000100000	00000
Ancyloscelis	001001100	1000011100	0000110001	0010211000	0100001001	0122210030	8000000200	0000000300	01000
Ptilothrix	011010100	0010000000	0000210001	0010111000	0100001001	0011110010	4000000300	0000000310	01000
Ancyla	100000000	0000010111	1010110000	0000101100	0201001001	00?3110002	0000000300	0011110000	01000
Tarsalia	101000110	1000011111	1010100001	0000111100	0201011001	0011110012	0000000310	0010110000	01000
Eucerinoda	011001110	1000010111	0000201000	0000111000	0201100000	001111001?	4000001820	0000110000	01000
Melissodes	001000111	1000011100	0000001101	0000111000	0201110000	0102210000	4000010800	0000010000	01000
Teratognatha	111000100	1001011000	0000100001	1000100000	3201101000	0103110020	2000000120	0000110100	01000
Chilimalopsis	?11200100	0000011100	0000200001	0000011000	3203101000	0103110000	2000000120	0001110100	01000
C.impressifrons	111000100	1000001000	0000200001	0000011000	3101101000	0003110010	2000000120	0001110100	01000
Eremapis	111002100	1011011100	1100100000	0000200000	0200101000	0103110010	5000001100	0000000400	01000
Isomalopsis	101002110	1011111100	0100000000	0000200110	0202111101	0101110120	9000010720	0000000400	00000
euphorbiae	101002100	1001111100	1100000100	0100211110	0202111001	0101110100	3000011400	0000000000	10100
albata	101002110	1?11111100	1110000000	0100211110	0202111011	0121110120	3000011500	0000200000	10100
compactula	101002110	1011111101	1111000101	0000211110	0202111011	0011110100	3000011500	0000000400	10100
completa	101002110	1011111101	1111000101	0000211110	0202111011	0011110100	3000011500	0000000400	10100
pygmaea	101002110	1001101100	0000100100	0000200120	0203111001	0101110020	3000010700	0000020500	10100
sidae	100002100	1001101100	0000100100	0100200120	0203101001	0103110020	3000010700	0000020500	10100
micheneri	101002100	1001101100	0000200100	0100200120	0203111001	0121110020	3010011700	0000020500	10100
texana	101002100	1001111100	0000100100	0100200120	0203111001	0101110020	3010011700	0000020500	10100
consobrina	101002100	1001111100	0000100100	0000201120	0203111001	0001110020	30?00????0	0000020500	10100
pallidicornis	101002100	1101111100	0100100100	0000211121	0203111001	0001110020	3010011700	0000020500	10100
solani	101002100	1000100000	0000101100	0100200111	0203111100	1100211020	1000110600	1001000001	01010
birkmanni	101002100	1000100000	0000101100	0100200111	0203111100	1100011020	1000110600	100100000?	01010
byersi	101002100	1000100000	0000001100	0100200111	0203111100	1100011020	1000110600	1001000001	01010
solitaria	101002111	1111100000	0000101101	0100200111	0203111101	0101110020	0000210401	1000100001	01000
aureosericea	101002111	1011100000	0000001101	1100200111	0203111101	0103330020	0001210410	1000100001	01001
trifasciata	101002111	1011100000	0000001001	0100200111	0203111101	0101110020	0001210410	1001000001	01001
jenseni	101110111	1001100000	0000101000	0100201111	0203111100	0101110020	0001210410	1001000000	01001
snowi	101110111	1001100000	0000001000	1100200111	0203111101	0102220020	0001210410	1001000001	01001
bicellularis	101002110	1111100000	0000101100	0100200111	0203111002	1100010020	6000011900	1000000201	01000
auropilosa	101002111	1111100000	0000101171	0100200111	0203111002	1103110021	0100010701	1100002200	01000
mourei	101002111	1111100000	0000001100	0100200111	0203111002	0103110021	0000010701	1100002200	00000
similis	101002111	1111100000	0000001101	0100200111	0203111002	0103110021	0000010701	1000000200	00000
mellipes	101002111	1111100000	0000001101	1100200111	0203111101	0022220021	0000010701	1100001200	01000
campestris	101002111	1111100000	0000101101	0000200111	0203111002	0122220021	0000010700	1100001200	01000
tomentosa	101002111	1111100000	0000001101	1200200111	0203111002	0100110021	0100010701	1100001200	01000
pulchella	101002111	1111100000	0000001111	1200200111	0203111002	?103220021	0000010701	1100001200	00000
vernoniae	101002111	1111100000	0000001111	1200200111	0203111101	1100030021	0000010701	1100001200	00000
analis	101002111	1111100000	0000001111	1200200111	0203111002	0003110021	0000010701	1100001200	00000
bruesi	101002111	1111100000	0000101171	0200200111	0203111002	0003110021	0000010701	1100001200	00000
fulvofasciata	101002111	1111100000	0000101111	1200200111	0203111101	0021110021	0000010701	1100001200	01000

lopsis (Phanomalopsis) jenseni and related species, the two arms of the apical process of S-8 are much more complex than in other basal species of this clade, such as *E. solitaria* and *E. aureosericea.*

Stilbomalopsis is supported by five unique synapomorphies: the presence of apical bands on T-1 to T-4 of females (character 56-1;); the subquandrangular disc of S-7 of males, whose lateral edges diverge toward the apex (character 60-1; Fig.8b); the narrow, transverse apical sclerite of S-7 of males (character 64-1; Fig.8b, *ap*); the apical process of S-8 of males, which is composed of a single broad lobe separated from the disc by a long stalk (character 67-6; Fig.9e) and the ventral lobe of the penis valve (character 83-1; Fig.11b, *vl*). In some trees, character 67-6 is shown as a synapomorphy of *Stilbomalopsis* + *Diomalopsis.* This is not likely to be so, though, since *Diomalopsis* has character 67-9 instead. A ho-

moplastic character supporting this clade is lateral ocelli of female entirely below the summit of the head (character 13-0; Fig.3a). This occurs, among other Exomalopsini, only in *Exomalopsis*.

The clade formed by *Exomalopsis s.s.* + *Megomalopsis* is supported by only one unique synapomorphy: the median elevated area of S-6 of males, which broadens toward the apex of the sternum, forming a carina or spine at each side (character 59-1). The long arms of the gonocoxite (character 71-1; Fig.10, *ag*) are a unique feature of all *Exomalopsis s.s.* + *Megomalopsis*, except *E. similis*. In those topologies in which *E. similis* is not the first branch of this clade, this feature is shown as a unique synapomorphy for the group. When *E. similis* is the first branch, this feature is a synapomorphy of the rest of the clade. Similarly, the expansion of the apex of the gonocoxite, enclosing the base of the gonostylus (character 76-1; Fig.14, *de, ve*), may be a synapomorphy of this clade. It is modified in *E. auropilosa, E. mourei* and *E. similis* and does not appear as a synapomorphy for the clade in topologies in which these species are the basal branches of the group.

Megomalopsis, represented by *Exomalopsis fulvofasciata* and *E. mellipes*, either appears as a polyphyletic lineage inside *Exomalopsis s.s.* (*sensu* Michener & Moure, 1957) or makes *Exomalopsis s.s.* paraphyletic and, thus, should not be retained as a taxonomic unit.

Diomalopsis is known from a single species and thus is characterized only by autapomorphic features. Its status as a subgenus of *Exomalopsis* may be retained, since it does not make any other group paraphyletic.

The clade comprising *Phanomalopsis s.s.*, *Stilbomalopsis*, *Diomalopsis* and *Exomalopsis s.s.* (from now on, *Exomalopsis s.l.*) is supported by two unique synapomorphies: the dorsal flange of the gonocoxite (character 70-1; Figs.11a, and 14, *df*) and, in some trees, the lobe of the posterior (distal) margin of the bridge of the penis valves (character 79-1; Figs.11a and 17a). This character, however, is reversed in *Exomalopsis s.s.* Other characters supporting that clade are: labrum and clypeus of male without yellow-pigmented areas (characters 16-0 and 17-0); propodeal articulating orifice directed downward on an oblique plane (character 26-1; Fig.5d,e) and the central velvet-like pilose area of the basitibial plate of females (character 39-1). Characters 16-0 and 17-0 are the common state among the basal lineages of the bees included in this study, but appear nowhere else among the Exomalopsini (as defined above). Character 26-1 appears independently in the Eucerini. Character 39-1 curiously appears also in *Anthophorisca pallidicornis*.

When all characters receive equal weights, two alternative hypotheses exist regarding the relationships among *Phanomalopsis, Stilbomalopsis* and *Diomalopsis* + *Exomalopsis s.s.* In the first hypothesis, *Diomalopsis* and *Stilbomalopsis* form a clade which is the sister group for another clade composed of *Phanomalopsis* and *Exomalopsis s.s.* (Fig.21). In the second hypothesis, *Phanomalopsis* is the basal branch, followed by *Stilbomalopsis* and by *Diomalopsis* + *Exomalopsis s.s.* (Fig.22). Among the trees generated after successive approximations, a third hypothesis (along with the second one) appears. In this third hypothesis, *Phanomalopsis* is sister to *Stilbomalopsis*, while *Diomalopsis* and *Exomalopsis s.s.* constitutes another lineage (Fig.23).

In the first hypothesis, the sister group relationship between *Diomalopsis* and *Stilbomalopsis* is not supported by any unique character. Three features supporting this clade are the lack of punctation and hairs on the disc of the first tergum of females (character 50-1) and the lack of tomentum on the marginal areas of T-2 and T-3 of females (characters 53-0 and 54-0). All of these occur in species of *Exomalopsis s.s.* The last character to support this clade is the lobe on the posterior margin of the dorsal bridge of the penis valves (character 79-1; Figs.11a and 17,a). This is also present in all *Phanomalopsis* and could well be a synapomorphy for all *Exomalopsis s.l.* that is reversed in *Exomalopsis s.s.*

In the same hypothesis, the sister group relationship between *Phanomalopsis* and *Exomalopsis s.s.* is supported by the excavation of the area between the lateral ocelli and the eyes of females (character 9-1; Fig.1a,c), by the convex or flat vertex of females (behind the summit of head - character 11-1; Fig.1c) and by the lack of a well delimited shining, non-punctate area above the propodeal pit of females (character 29-1). Character 9-1 is unique to these groups in Exomalopsini, but is present in other taxa like the Tapinotaspini, *Melissodes* and *Tetrapedia*. Character 11-1 is present, among the species of *Phanomalopsis*, only in *Exomalopsis solitaria*. Character 29-1 is the most common condition in the outgroup taxa and is reversed in *Exomalopsis mourei*.

In the second hypothesis, the sister group relationship between *Stilbomalopsis* and the *Diomalopsis* + *Exomalopsis s.s.* lineage is supported by the following features: punctation present on disc of T-I of female, between the dorsolalteral convexities (character 50-1); and absence of tomentum on the marginal area of T-2 and T-3 of female (characters 53-0 and 54-0). Character 50-1 is not constant within *Exomalopsis s.s.* Characters 53-0 and 54-0 each occurs in only one species of *Exomalopsis s.s.*

In the third hypothesis, the sister-group relationship between *Phanomalopsis* and *Stilbomalopsis* is supported by the depression of the premarginal line of T-1 of females, forming a transverse sulcus (character 47-1), and by the expanded posterior margin of the dorsal bridge of the penis valves (character 79-1; Fig.11a and 17a). Character 47-1 is also present in several species of *Exomalopsis s.s.* and in *Isomalopsis*. Character 79-1 is also present in *Diomalopsis* and could be claimed, equally parsimoniously, to be a plesiomorphic feature of all four lineages of *Exomalopsis s.l.* that reversed in *Exomalopsis s.s.*

In the second and third hypotheses, the sister-group relationship between *Exomalopsis s.s.* and *Diomalopsis* is supported by two unique characters: the reduction of the disc of female T-1, which is less than one-third as long as the marginal area (character 49-2), and the short gonostylus that is triangular in profile, broader basally (character 77-2; Fig.14).

The only relationship between any two groups among the lineages of *Exomalopsis s.l.* that is well supported is the one between *Diomalopsis* and *Exomalopsis s.s.* The positions of *Phanomalopsis* and *Stilbomalopsis* are not well defined.

Classificatory Proposals

The main concern while making classificatory decisions in this study was to be consistent with the phylogenetic hypothesis reconstructed for the groups involved (Hull, 1964). For this reason, only monophyletic taxa (*sensu* Hennig, 1966) were accepted. Whenever monophyly of groups was not violated, sinking established taxa or proposing new ones was avoided, so that taxonomic stability was maximized.

The first main classificatory change proposed here is the exclusion of *Chilimalopsis* and *Teratognatha* from the Exomalopsini, and the recognition of a new tribe for them. The acceptance of *Chilimalopsis* and *Teratognatha* as part of the Exomalopsini would make this tribe polyphyletic. Even considering that a sister-group relationship between those genera and Eucerini is not strongly supported, their unique synapomorphies justify a new tribe. Other changes presented here regard reformulation of the generic and subgeneric classification of Exomalopsini.

Tribe TERATOGNATHINI, new tribe

Minute and slender bees. Body black, except in males labrum and, in some cases, apical margin of clypeus yellow. Hairs generally sparse and short; scopa sparse, composed of minutely and sparsely branched hairs; maxillary palpus six-segmented (five-segmented in *Chilimalopsis impressifrons* and in male *Teratognatha modesta*); mandible with subapical tooth; labrum of female without median longitudinal line flanked by rows of erect hairs; clypeus weakly convex to weakly protuberant; internal margin of eye not margined by paraocular cilia; postocellar ridge absent; marginal cell obliquely truncate apically (round, separating from wing margin in a gentle curve in *Chilimalopsis* sp.), longer than distance between its apex and wing tip; pterostigma small, less than three times as long as prestigma (longer in *Teratognatha*), its margin, inside marginal cell, straight or gently convex; pygidial plate present in females and in male *Chilimalopsis* sp., indicated by transverse recurved carina in male *C. impressifrons* and absent in *Teratognatha*; S-7 of male pentagonal; anterior edge of S-8 of male pointed; internal wall of gonocoxite with peglike setae, subapically, and narrow apical process above gonostylus and directed dorsad; gonostylus relatively long and slender, originating in apicolateral projection of gonocoxite and extending in an axis parallel to that of gonocoxite. Restricted to the semi-arid regions of Argentina and Chile and, perhaps, Bolivia and Paraguay.

Two genera are currently recognized in this tribe: *Teratognatha* Ogloblin (containing a single species, *T. modesta* Ogloblin) and *Chilimalopsis* Toro (containing *C. parvula* Toro and *C. impressifrons* Roig-Alsina). It seems that the species referred to as *Chilimalopsis* sp. in this paper is an additional undescribed species from Chile. In the analyses above *Chilimalopsis impressifrons* appeared to be more closely related to *Teratognatha modesta* than to *Chilimalopsis* sp., which renders the genus *Chilimalopsis* paraphyletic. For this reason, the generic classification of the Teratognathini is not treated here, but will be subject of a separate detailed study.

Tribe EXOMALOPSINI

Taxonomy: Michener,1944:271; Michener & Moure,1957:405; Michener,1974:23,28; 1979:278,287,314,332,333,335; Hurd,1979:2115; Roig-Alsina & Michener,1993:155; Silveira,1993.
Biology: Rozen,1984.

Minute to small bees, generally robust. Body black, except for yellow labrum and clypeus of *Eremapis* and of male *Anthophorula s.l.* and for red metasoma in some *Anthophorula* and *Exomalopsis*. Hairy, pubescence often long; scopa dense, composed of long hairs coarsely plumose to apices. Maxillary palpus six-segmented (five-segmented in *Eremapis*); labrum of females (except in some *Phanomalopsis*) with a median longitudinal line, sometimes elevated, flanked by rows of erect hairs; mandible (except in *Eremapis*) simple, without subapical tooth; clypeus flat or weakly convex; internal margin of eye (escept in *Eremapis*) margined by paraocular cilia; postocellar ridge absent or present; marginal cell obliquely truncate apically, longer than distance between its apex and wing tip; pterostigma large (short in *Anthophorula s.s.*), its margin, inside marginal cell, gently convex or truncate; pygidial plate present in females and in males of *Anthophorula s.s.*, absent on male *Eremapis*, suggested by an apical recurved carina in male *Isomalopsis*, *Anthophorisca* and *Exomalopsis s.l.*; shape of S-7 of males variable but not pentagonal; anterior edge of S-8 of male straight or broadly convex medially (pointed in *Eremapis*); internal wall of gonocoxite simple, without apical process (except in *Exomalopsis solitaria* and *E. aureosericea*) or peglike setae subapically; gonostylus variable in shape, but always originating on the apex of gonocoxite and extending in the same axis as gonocoxite. Mostly neotropical, occurring from northern Argentina to western and central U.S.A.

Genus *Eremapis* Ogloblin

Eremapis Ogloblin,1956:149; Michener & Moure,1957:405,435; Roig-Alsina,1992:152. Type species: *Eremapis parvula* Ogloblin,1956 (original designation).

This genus was well described by Ogloblin (1956) and again by Michener & Moure (1957). It consists of a single species, *E. parvula*, from Argentina.

Genus *Anthophorula* Cockerell

Anthophorula is again raised to generic rank. Here, however, it is expanded to include not only the North American *Anthophorula s.s.* and *Anthophorisca*, but also the South American *Isomalopsis*. The close affinity between *Isomalopsis* and *Anthophorula* was already noted by Michener & Moure (1957).

Labrum and clypeus of male yellow (except in *Anthophorisca levigata* and *A. linsleyi*); area between lateral ocellus and eye convex; postocellar ridge absent; superior margin of eyes below level of summit of head in *Anthophorisca*, above in *Isomalopsis* and most *Anthophorula s.s.*; basitibial plate of female small, its surface flat and uniformly hairy (except in *Anthophorisca pallidicornis* as in *Exomalopsis*); transverse carina of T-1 of female present (weak or sometimes absent in *Anthophorisca*), that of male present in *Anthophorula* and *Isomalopsis*; disc of S-7 of male bilobed, much broader than long (in *Isomalopsis* base of lobes broadened and apodemes reduced); penis valves narrow, dorsal edges closer to each other than ventral ones (except in *Isomalopsis*); dorsal flange of gonocoxite absent.

Subgenus *Isomalopsis* Michener & Moure (new status)

Isomalopsis Michener & Moure,1957:405,434. Type species: *Tetralonia niveata* Friese,1908 (original designation).

This subgenus was described and illustrated by Michener & Moure (1957) as a separate genus. It is currently known from a

single species, *I. niveata*, from Argentina. I have seen specimens identified by Moure as belonging to a second undescribed species. I did not make a detailed comparison between it and *I. niveata* and, without detailed study, I could not distinguish it from *I. niveata*.

Subgenus *Anthophorula* Cockerell *sensu stricto*.

Anthophorula Cockerell,1897:44; 1898:42,70; Lutz & Cockerell,1920:564; Michener,1951: 1187; Michener & Moure,1957:432; Hurd,1979:2116; Timberlake,1980:3-37,43. Type species: *Anthophorula compactula* Cockerell,1897 (original designation).

Dadasella Ashmead,1899:64. Type species: *Dadasella coquilletti* Ashmead,1899 (= *Synhalonia albicans* Provancher) (original designation and monobasic).

Pachyerapis Cockerell,1922:4. Type species: *Exomalopsis (Pachyerapis) cornigera* Cockerell,1922 (original designation and monobasic).

This group is well characterized in Michener & Moure (1957) as *Exomalopsis (Anthophorula)*. Timberlake (1980) recognized 29 species in this subgenus and provided a key for their identification. Species of *Anthophorula* occur in Mexico from Hidalgo and Jalisco northward into the U.S.A., to Oregon in the west and Texas in the east.

Subgenus *Anthophorisca* Michener & Moure

Anthophorisca Michener & Moure,1957:433; Hurd,1979:2118; Timberlake,1980:39-73. Type species: *Melissodes pygmaea* Cresson,1872 (original designation).

Panomalopsis Timberlake,1980:82. Type species: *Exomalopsis linsleyi* Timberlake,1980 (original designation). New synonym.

This group is well described in Michener & Moure (1957), and a useful key for its species is provided by Timberlake (1980). This group includes the subgenus *Panomalopsis*, erected by Timberlake (1980) for *Exomalopsis linsleyi*. This species is known only from the male holotype and, for this reason, was not included in the phylogenetic analyses. I have examined the type specimen and regard it as being a derived *Anthophorisca*. With the inclusion of *A. linsleyi*, *Anthophorisca* comprises 30 species. Species of *Anthophorisca* occur from Oaxaca, in Mexico, northward into the U.S.A., to California in the west, Indiana and Mississipi in the east, and Nebraska in the north.

Genus *Exomalopsis* Spinola

Exomalopsis Spinola,1853:89; Smith,1854:364; 1879:125; Taschenberg,1883:82; Dalla Torre,1896:298; Cockerell,1898:42,71; Friese,1899:247; Ashmead,1899:64; Schrottky,1902: 525; 1913:262; Ducke,1906:59;1912:97; Brèthes,1909:223; Lutz & Cockerell,1920:564; Michener,1941:301; 1944:272; 1951:1187; 1974:28; 1979:314,317,334,336; Michener & Moure, 1957:405, 427; Timberlake, 1947,1980; Mitchell,1962:235; Michener *et al.*,1994: 158.

The scope of this genus is restricted here by the exclusion of *Anthophorula* and *Anthophorisca*. Its species can be characterized by the following set of features:

Labrum and clypeus of male dark as in female; pterostigma large, two-thirds as long as marginal cell on wing margin or more, its apex sometimes truncate; basitibial plate of female large, with central pilose area separated by groove from raised margin; transverse carina of T-1 present on females, absent from males (except in some *Phanomalopsis*); premarginal line of T-1 of female evident or not, sometimes depressed, forming groove; S-7 and S-8 and genitalia of male highly variable, dorsal flange of gonocoxite present.

Subgenus *Stilbomalopsis* new subgenus

Type species: *Exomalopsis solani* Cockerell,1896.

This group of species was included by Michener & Moure (1957) in their subgenus *Phanomalopsis* and was considered as such by Timberlake (1980). It can be characterized by the following set of features:

Small, robust, hairy bees. Body black. Labrum flat with apical margin gently curved (except in *arcuata*, in which the surface is slightly concave and the margin pointed); clypeus flat; vertex in frontal view convex; area between lateral ocellus and eye not excavated (except in *arcuata*), bare and shining or with minute punctures and hairs; superior margin of eye below level of vertex behind it; postocellar ridge absent; propodeum with large well-defined shining area medially; pterostigma large (at least three times as long as prestigma), generally truncate apically; disc of T-1 of female one-third as long as marginal zone or more; disc of T-1 and marginal zones of T-1 and T-2 (sometimes also T-3 and T-4) bare, impunctate and shining; apical fimbria of T-2 to T-4 dense and soft, generally white, sometimes interrupted medially. S-6 of male entirely flat; disc of S-7 of male subquadrangular, its lateral edges arcuate, closest to each other medially; ventral lobe of penis valve present; apical process of S-7 of male present as narrow transverse sclerite fused laterally to arms of disc; apical process of S-8 of male a single bare lobe.

Eleven of the species listed by Timberlake (1980) as *Phanomalopsis* belong in this group (*affabilis* Timberlake, *arcuata* Timberlake, *bimotata* Timberlake, *birkmanni* Cockerell, *byersi* Timberlake, *dimidiata* Timberlake, *hurdi* Timberlake, *limata* Cresson, *pueblana* Timberlake, *solani* Cockerell, *solidaginis* Cockerell). Among these, *arcuata* is unusual for the excavated area between the lateral ocellus and eye and for the concave, pointed labrum of the female. The male also has unusual features on S-7 and S-8 as well as in the gonocoxite. Additionally, *aequabilis* and *notabilis*, probably fit here. *Exomalopsis bakeri* seems to be an *Exomalopsis s.s.* The species of *Stilbomalopsis* can be identified with the help of Timberlake's key. *Stilbomalopsis* occurs in Central America, from El Salvador and Nicaragua, northward through Mexico to California, Arizona, New Mexico and Texas in the U.S.A.

Etymology: from the Greek words *stilbo* (glitter, shine); *homalos* (flat); *opsis* (face). "A shining *Exomalopsis*". The name refers to the smooth and shining abdominal terga.

Subgenus *Phanomalopsis* Michener & Moure

Phanomalopsis Michener & Moure,1957:430; Hurd,1979:2116; Timberlake,1980:79,83. Type species: *Exomalopsis jenseni* Friese,1908 (original designation).

This subgenus is restricted here, compared to its definition by Michener & Moure (1957), by the removal of *Exomalopsis solani* and related species to *Stilbomalopsis*. Three grades can be identified in *Phanomalopsis*. One is composed of two small species, *E. solitaria* and *E. diminuta*; another by *Exomalopsis aureosericea*, *E. trifasciata* and *E. atlantica;* and the third by *Exomalopsis jenseni* and related species. Only the third group is supported as a monophyletic assemblage by synapomorphic features. The first two groups retain many plesiomorphic features which make this subgenus difficult to characterize without using male genitalia.

Labrum and clypeus of male dark; vertex of head of females, in frontal view, in straight lines; lateral ocelli above summit of head; area between lateral ocelli and eye broad, gently excavated (more so in males); postocellar ridge absent or very weakly-developed; superior margin of eyes of females below (sometimes almost at the same level as) summit of head behind it; premarginal line of T-1 of female depressed, forming groove; disc of T-1 of female punctate and pilose (sometimes only partially), at least one-third as long as marginal area; marginal area of T-1 of female glabrous and shining, except sometimes for area behind dorsolalteral convexities. S-6 of male entirely flat; apical process of S-7 complex, with two

basi-lateral lobes on the ventral surface; apical process of S-8 produced into two long arms, sometimes with hairs and complex accessory lobes.

Phanomalopsis comprises 10 species. Most of them occur in the pampa and semidesertic areas of northern Argentina, Bolivia and Paraguay. A single species, *E. (P.) snowi* occurs from the Caribbean coast of Venezuela and Colombia, through Panamá, Guatemala, Mexico to southern Texas in the U.S.A. A small group of species exists in southern and southeastern Brazil. No species is known to occur in the savannas of central Brazil or in the Amazonian basin.

Subgenus *Diomalopsis* Michener & Moure

Diomalopsis Michener & Moure,1957:431. Type species: *Exomalopsis bucl lularis* Michener & Moure,1957 (original designation)

This group was well described by Michener & Moure (1957) and is known from a single species which occurs only in the Atlantic Forest on the southeastern Brazilian coast. An additional undescribed species from eastern Paraguay and southwestern Brazil seems to fit in this subgenus. I have seen only females of this species and an examination of male genitalia would be necessary to confirm its position.

Subgenus *Exomalopsis* Spinola *sensu stricto*

Exomalopsis Michener,1951:1187; Michener & Moure,1957:428; Hurd,1979:2115; Timberlake, 1980:119. Type species: *Exomalopsis auropilosa* Spinola,1853 [by designation of Taschenberg, 1883:82 (as *E. fulvopilosa*)].

?Epimonispracto Holmberg,1903:426. Type species *Epimonispracto gratosus* Holmberg,1903 (original designation).

Megomalopsis Michener & Moure,1957:430; Timberlake,1980:79,101. Type species *Exomalopsis diversipes* Cockerell,1949 (original designation). New synonym.

This group is redefined here to comprise the species placed by Michener & Moure (1957) and Timberlake (1980) in both *Exomalopsis* s.s. and *Megomalopsis*.

Outline of summit of head, in frontal view, between lateral ocellus and eye, straight; area between lateral ocellus and eye excavated; postocellar ridge present (sometimes limited to area just at sides of lateral ocelli); area above propodeal pit punctate as rest of propodeum (shining in *mourei*); disc of T-1 of female less than one-third as long as marginal zone; S-6 of male with median elevated area broadening toward apex, forming carina or spine at each side; disc of S-7 of male subtriangular with no apical process; apical process of S-8 short, produced as two apical projections; gonocoxite long, almost reaching tips of penis valves; gonostylus arising from an invagination produced by expansion of apex of gonocoxite; dorsal flange placed apically on gonocoxite.

This is the most speciose group of Exomalopsini and the one whose species-level taxonomy is least studied. There are about 50 valid species in this subgenus (Silveira, 1995). A revision of this group, however, will certainly reveal new synonymies and new species. It occurs from northern Argentina to southwestern U.S.A., both in semidesertic and forested areas. The last comprehensive study to consider the faunas of all the Americas together was that of Friese (1899). Timberlake (1980) reviewed the species of North and Central America, but his work is badly in need of revision. Furthermore, his key was published with many mistakes which make it almost impossible to use. After Friese's (1899) paper no revision was made of the South American species, but new species were described in inumerous isolated papers or in accounts of regional bee faunas. The location of the types of several of these is currently unknown.

KEY TO THE GENERA AND SUBGENERA OF EXOMALOPSINI

(Note: this key ends in a triplet instead of a couplet).

1. Second medial cell of forewing about as long as second cubital; labrum and clypeus of female yellow; T-7 of male produced into a broad sharp carina; S-7 of male trilobed ..... *Eremapis.*
—. Second medial cell of forewing distinctly shorter than second cubital; labrum and clypeus of female entirely dark; margin of T-7 of male not produced into a carina, or *if* a carina is present, then its posterior margin is recurved; S-7 of male not trilobed 2
2. Basitibial plate of female with surface flat; *if* margins of plate are raised, then transverse carina of T-1 of female absent; labrum and clypeus of male yellow or white [except in *Anthophorula (Anthophorisca) levigata* and *A.(Anthophorisca) linsleyi*]; outer side of penis valve without lateral process; dorsal flange of gonocoxite absent (*Anthophorula s.l.*) 3
—. Basitibial plate of female with raised margin (generally separated from central pilose area by groove); transverse carina of T-1 of female present; labrum and clypeus of male entirely dark; outer side of penis valve with lateral process; dorsal flange of gonocoxite present (*Exomalopsis s.l.*) 5
3. Transverse carina of T-1 of female weak or absent; that of male absent; peglike setae present on apex of gonocoxite (except in *A. linsleyi*, which has strong pointed setae instead) ..... *Anthophorisca.*
—. Transverse carina of T-1 of female strong; that of male present; peglike setae absent from apex of gonocoxite 4
4. Pterostigma large, 4 times as long as prestigma, its inner breadth much greater than breadth of its marginal veins; yellow marks on clypeus of male absent or restricted to an apical transverse line; S-6 of male with two lateral flanges which bear a series of spicules on their inner margins ..... *Isomalopsis.*
—. Pterostigma small, no more than 3 times as long as prestigma, its inner breadth as large as or smaller than breadth of its marginal veins; clypeus of male entirely yellow; S-6 of male simple ..... *Anthophorula s.s.*
5. Vertex in frontal view convex; area between lateral ocellus and eye not excavated (except in *E. arcuata*) and lateral ocelli below level of summit of head; marginal zones of T-1 and T-2 of female smooth and glabrous; T-2 to T-4 of female with white, dense, apical fasciae, sometimes interrupted medially; apical process of S-7 of male present as narrow transverse sclerite fused laterally to arms of disc; apical process of S-8 of male a single bare lobe ..... *Stilbomalopsis.*
—. Vertex in frontal view straight; area between lateral ocellus and eye excavated and/or lateral ocelli above level of summit of head; marginal zone of T-1 and/or T-2 of female punctate and pilose; T-2 to T-4 of female with apical fasciae absent or present; apical process of S-7 of male absent or complex and with two free

basilateral lobes under ventral surface; apical process of S-8 bearing two apical arms (short or long); *if* a single broad lobe, than lobe is hairy 6

6. Three submarginal cells; vertex of female between ocellus and eye gently excavated (more so on males); postocellar ridge absent (but summit of head sometimes narrow); premarginal line depressed on T-1 of female, forming transverse sulcus, *and* marginal zone between dorsolateral convexities smooth and shining, comprising no more than two-thirds of dorsal surface of tergum; S-6 of male entirely flat . . . . *Phanomalopsis.*

—. Three submarginal cells; vertex of female between ocellus and eye excavated; postocellar ridge present, sometimes limited to portions just to sides of lateral ocelli; *if* premarginal line depressed on T-1 of female, then marginal zone between the dorsolateral convexities punctate *and/or* comprising much more than two-thirds of dorsal surface of tergum; S-6 of male with median elevated area that broadens toward apex of sternum, forming a carina or spine at each side; S-7 and S-8 of male without peg-like setae . . . . . *Exomalopsis s.s.*

—. Two submarginal cells; vertex of female between ocellus and eye not excavated; postocellar ridge absent; premarginal line on T-1 of female not depressed; S-6 of male entirely flat; S-7 and S-8 of male with peg-like setae . . . . . *Diomalopsis.*

DISCUSSION AND CONCLUSIONS

Phylogenetic Considerations

The understanding of the relationships among the taxa formerly included in the Anthophoridae has recently changed greatly. The scope of Exomalopsini was greatly modified by Roig-Alsina & Michener (1993) and by the removal of the Teratognathini in this paper. Changes have been drastic enough to make meaningless previous statements (*e.g.*,Michener, 1944; Michener & Moure, 1957) about Exomalopsini being the most primitive branch of the Anthophorinae (*sensu* Michener, 1944;) or the Apinae (*sensu* Roig-Alsina & Michener, 1993). The results obtained here offer a new hypothesis for the relationships of Exomalopsini. As redefined here, Exomalopsini would not be the most primitive branch of Apinae, but the sister taxon of a group including Ancylini, Eucerini and the newly proposed Teratognathini.

The Ancylini, once suspected to be closely related to or part of the Exomalopsini, (Michener, 1944; Michener & Moure, 1957; Silveira, 1993) appears here to be more closely related to the Eucerini. This was already suggested by Roig-Alsina & Michener (1993). *Tarsalia* appeared at the base of Eucerini in some of the trees obtained by those authors, who argued that the Ancylini could indeed be a basal branch of the Eucerini. Here, the monophyly of the Ancylini receives additonal support and Teratognathini is hypothesized to be the sister-group of the Eucerini. The relationship of Teratognathini to Eucerini, however, is not strongly supported.

Exomalopsini as here defined contains three genera: *Eremapis*, *Anthophorula* (with the subgenera *Anthophorula s.s.*, *Anthophorisca* and *Isomalopsis*) and *Exomalopsis* (with the subgenera *Exomalopsis s.s.*, *Diomalopsis*, *Phanomalopsis* and *Stilbomalopsis*).

Relationships among the subgenera of *Anthophorula* were consistent throughout the analyses: *Anthophorisca* is the sister-group of a clade composed of *Isomalopsis* and *Anthophorula s.s. Panomalopsis linsleyi* Timberlake is considered to be a highly derived *Anthophorisca* and is included in that subgenus.

The subgenera of *Exomalopsis* are consistent groups. Only *Phanomalopsis*, with a few basal species that retain many of the plesiomorphies for the clade, cannot be sharply separated from the others. It seems quite possible that *Diomalopsis* and *Exomalopsis s.s.* are sister taxa, but the relationships between them and the other subgenera are not clear.

Biogeographic Considerations

The idea of a close relationship between Ancylini and Exomalopsini (*e.g.* Michener, 1944; Michener & Moure, 1957) posed a biogeographic puzzle: Ancylini are restricted to the xeric strip of land extending from the Mediterranean basin to central Asia, while Exomalopsini are restricted to the western hemisphere. The phylogenetic hypothesis resulting from the present analyses transfers the biogeographic puzzle from the relationship between Ancylini and Exomalopsini to the relationships among a greater number of taxa. The topology for the tribes of Apinae employed as outgroups shows successive branches alternating between groups currently occurring in the western and eastern hemispheres and does not seem to contribute to the elucidation of the biogeographical history of the subfamily.

The phylogenetic relationships among the groups of Exomalopsini as defined here and their geographical ranges suggest a complex biogeographic history that may include major vicariant events along with dispersal through xeric corridors in past drier times in the Americas.

Eremapis, the most basal extant lineage of Exomalopsini, is restricted to temperate South America. This supports the belief of a South American origin for the tribe (Michener, 1944, 1979; Michener & Moure, 1957). However, it is possible that *Eremapis* is just a remnant of a once widespread lineage. The sister-group relationship between *Isomalopsis* and *Anthophorula s.s.* suggests that the ancestral stock of *Anthophorula* was widespread throughout the Americas at a time in which xeric climates were prevalent. Other examples of bee taxa presenting this amphitropical distribution are, according to Michener (1979), the genera and subgenera *Ptilothrix* and *Dasiapis* (Emphorini), *Martinapis* (Eucerini) and *Xerocentris* (Centridini). The existence of several amphitropical taxa occurring in xeric areas of both temperate regions of the Americas suggests one or more major opportunities for faunistic interchange between the southern and the northern continents. It has already been suggested that part of this interchange might have occurred before

the union of the Americas (Michener, 1979).

Among the lineages of *Exomalopsis*, *Stilbomalopsis* is restricted to Central and North America northward to southwestern United States and probably originated there. Most species of *Phanomalopsis*, including its basal lineages, are in South America and this is probably where they originated. The origin of *Exomalopsis s.s.*, however, is less clear, since there is not a consensus hypothesis about the basal branches in the lineage. Acceptance of a sister-group relationship with *Diomalopsis* would suggest a South American origin for the group.

The results of the phylogenetic analyses suggest a semidesertic habitat for the ancestral species of Exomalopsini. They suggest also that invasion of other habitats occurred relatively recently in the history of the tribe and has happened independently at least twice: once or more in *Phanomalopsis* and again in *Exomalopsis s.s. Eremapis* (the most basal lineage of the tribe), *Anthophorula s.l.* and the most basal lineages of *Exomalopsis s.l.* are mostly restricted to semi-desertic areas: *Eremapis* and *Isomalopsis* in temperate South America; *Anthophorisca*, *Anthophorula* and *Stilbomalopsis* in similar habitats in North America. Most *Phanomalopsis*, including one of its most basal extant species (*E. solitaria*), are restricted to arid areas (although other basal species, *E. aureosericea* and *E. atlantica*, live in forested habitats). Only *Diomalopsis* and most species of *Exomalospis s.s.* are restricted to moist tropical environments.

LITERATURE CITED

Ashmead, W.H. 1899. Classification of bees, or the superfamily Apoidea. Transactions of the American Entomological Society 26:49-100.

Brèthes, J. 1909. Notas Himenopterológicas. Anales del Museo Nacional de Buenos Aires 19:219-223.

Camargo, J.M.F., W.E. Kerr & C.R. Lopes. 1967. Morfologia externa de *Melipona* (*Melipona*) *marginata* Lepeletier (Hymenoptera, Apoidea). Papéis Avulsos do Departamento de Zoologia de São Paulo 20:229-258.

Camargo, J.M.F. & M. Mazucato. 1984. Inventário da apifauna e flora apícola de Ribeirão Preto, SP, Brasil. Dusenia 14:55-87.

Cockerell, T.D.A. 1896. *Exomalopsis*, a neotropical genus of bees in the United States. The Canadian Entomologist 28:25.

Cockerell, T.D.A. 1897. Life Zones in New Mexico. New Mexico College of Agriculture and Mechanic Arts Agricultural Experiment Station Bulletin no. 24:1-44.

Cockerell, T.D.A. 1898. Tables for the determination of New Mexico bees. Bulletin of the University of New Mexico 1:41-73. Also in the Bulletin of the Scientific Laboratories of Denison University 11:41-73.

Cockerell, T.D.A. 1899. Catálogo de las Abejas de México. México, Biblioteca Agrícola de la Secretaría de Fomento. 20pp.

Cockerell, T.D.A. 1922. Two new subgenera of North American bees. American Museum Novitates no. 47:1-5.

Dalla Torre, C.G. de. 1896. Catalogus Hymenopterorum Hucusque Descriptorum, Systematicus et Synonymicus. Vol.10: Apidae (Anthophila). Leipzig: Engelmann. 643pp.

Ducke, A. 1906. Neue Beobachtungen über die Bienen der Amazonasländer. Zeitschrift für Wissenschaftliche Insektenbiologie 2:51-60.

Ducke, A. 1912. Die natürlichen Bienengenera Südamerikas. Zoologisches Jahrbucher, Abteilung für Systematik, Geographie und Biologie der Tiere, 34:51-116.

Farris, J.S. 1969. A successive approximations approach to character weighting. Systematic Zoology 18:374-385.

Farris, J.S. 1988. Hennig86 Reference. Version 1.5. Port Jefferson Station, New York, distributed by the author.

Friese, H. 1899. Monographie der Bienengattungen *Exomalopsis*, *Ptilothrix*, *Melitoma* und *Tetrapedia*. Annalen des k.k. naturhistorischen Hofmuseums Wien 14:247-304.

Friese, H. 1908. Die Apidae (Blumenwespen) von Argentina nach den Reisenergebnissen der Herren A.C. Jensen-Haarup und P. Jörgensen in der Jahren 1904-1907. Flora og Fauna 10: 331-425 (p. 1-94 in reprint).

Hennig, W. 1966. Phylogenetic Systematics. Urbana: University of Illinois. xvi + 263p.

Hicks, C.H. 1936. Nesting habits of certain western bees. The Canadian Entomologist 68:47-52.

Holmberg, E.L. 1903. Delectus hymenopterologicus argentinus. Hymenopterum argentinum et quorumdam exoticorum observationes synonimicas, addendas, novorumque generum specierumque descriptiones continens. Anales del Museo Nacional de Buenos Aires (3)2:377-511.

Hull, D.L. 1964. Consistency and monophyly. Systematic Zoology 13:1-11.

Hurd, P.D., Jr. 1979. Apoidea. pp. 1741-2209 *in*: K.V.Krombein; P.D.Hurd, Jr.; D.R. Smith; B.D. Burks (eds.) Catalog of Hymenoptera in America North of Mexico. Vol. 2. Washington, Smithsonian Institution.

Hurd, P.D., Jr., W.E. LaBerge & E.G. Linsley. 1980. Principal sunflower bees of North America with emphasis on the Southwestern United States (Hymenoptera: Apoidea). Smithsonian Contributions to Zoology no. 310:1-158.

Linsley, E.G., J.W. MacSwain & R.F. Smith. 1954. A note on the nesting habits of *Exomalopsis solani* Cockerell. The Pan-Pacific Entomologist 30:263-264.

Lutz, F.E. & T.D.A. Cockerell. 1920. Notes on the distribution and bibliography of North American bees of the families Apidae, Meliponidae, Bombidae, Euglossidae, and Anthophoridae. Bulletin of the American Museum of Natural History 42:491-641.

McGinley, R.J. & J.G. Rozen, Jr. 1987. Nesting biology, immature stages, and phylogenetic placement of the Palaearctic bee *Pararhophites* (Hymenoptera: Apoidea). American Museum Novitates no. 2903:1-21.

Maddison, D.R. 1991. The discovery and importance of multiple islands of most-parsimonious trees. Systematic Zoology 40:315-328.

Michener, C.D. 1941. The distributional history of North American bees. Proceedings of the Sixth Pacific Science Congress. Vol. 4, p. 297-303.

Michener, C.D. 1944. Comparative external morphology, phylogeny, and a classification of the bees (Hymenoptera). Bulletin of the American Museum of Natural History 82:153-326.

Michener, C.D. 1951. Tribe Exomalopsini. pp 1186-1188 *in* Muesebeck, C.F.W.; K.V. Krombein & H.K. Townes (eds) Hymenoptera of America North of Mexico – Synoptic Catalog. Agriculture Monograph no. 2. Washington, USDA.

Michener, C.D. 1966. Evidence of cooperative provisioning of cells in *Exomalopsis* (Hymenoptera: Anthophoridae). Journal of the Kansas Entomological Society 39:315-317.

Michener, C.D. 1974. The Social Behavior of the Bees – a Comparative Study. Cambridge: Harvard University. xii + 404 pp.

Michener, C.D. 1979. Biogeography of the bees. Annals of the Missouri Botanical Garden 66: 277-347.

Michener, C.D., R.J. McGinley & B.N. Danforth. 1994. The Bee Genera of North and Central America (Hymenoptera: Apoidea). Washington: Smithsonian Institution. x + 209p.

Michener, C.D. & J.S. Moure. 1957. A study of the classification of the more primitive non-parasitic anthophorine bees (Hymenoptera, Apoidea). Bulletin of the American Museum of Natural History 112:395-452.

Mitchell, T.B. 1962. Bees of the Eastern United States, v.2. The North Carolina Agricultural Experiment Station Technical Bulletin No.152. p. 1-557.

Neff, J.L. 1984. Observations on the biology of *Eremapis parvula* Ogloblin, an anthophorid bee with a metasomal scopa (Hymenoptera: Anthophoridae). Pan-Pacific Entomologist 60: 155-162.

Nixon, K.C. & J.M. Carpenter. 1993. On outgroups. Cladistics 9:83-103.

Norden, B.B., K.V. Krombein & S.W.T. Batra. 1994. Nests and enemies of *Exomalopsis (Phanomalopsis) solani* Cockerell (Hymenoptera: Apoidea, Mutillidae; Diptera: Asilidae). Proceedings of the Entomological Society of Washington 96:350-356.

Ogloblin, A. 1956. Dos géneros nuevos de la tribu Exomalopsini (Apidae, Hym.) de la Republica Argentina. Dusenia 7:149-158.

Parker, F.D. 1984. Biological notes on the bee *Exomalopsis crenulata* Timberlake (Hymenoptera: Anthophoridae). Pan-Pacific Entomologist 60:188-192.

Popov, V.V. 1949. The tribe Pararhophitini (Hymenoptera, Anthophorinae) as an early Tertiary element of the recent desert fauna of central Asia and Egypt. Doklady Akademii Nauk SSSR 66:507-510. [in Russian].

Raw, A. 1976. Seasonal changes in the numbers and foraging activities of two Jamaican *Exomalopsis* species (Hymenoptera, Anthophoridae). Biotropica 8:270-277.

Raw, A. 1977. The biology of two *Exomalopsis* species (Hymenoptera: Anthophoridae) with remarks on sociality in bees. Revista de Biología Tropical 25:1-11.

Roig-Alsina, A.1992. La presencia de *Chilimalopsis* Toro en la Argentina y descripcion de una nueva especie (Hymenoptera, Anthophoridae). Neotropica 38(100):149-153.

Roig-Alsina, A. & C.D. Michener. 1993. Studies of the phylogeny and classification of long-tongued bees (Hymenoptera: Apoidea). The University of Kansas Science Bulletin 55:124-162.

Rozen, J.G., Jr. 1977. Immature stages of and ethological observations on the cleptoparasitic bee tribe Nomadini (Apoidea, Anthophoridae). American Museum Novitates no. 2638:1-16.

Rozen, J.G., Jr. 1984. Comparative nesting biology of the bee tribe Exomalopsini (Apoidea, Anthophoridae). American Museum Novitates no. 2798:1-37.

Rozen, J.G., Jr. & D. MacNeill. 1957. Biological observations on *Exomalopsis (Anthophorula) chionura* Cockerell, including a comparison of the biology of *Exomalopsis* with that of other anthophorid groups (Hymenoptera: Apoidea). Annals of the Entomological Society of America 50:522-529.

Schrottky, C. 1902. Ensaio sobre as abelhas solitárias do Brasil. Revista do Museu Paulista 5: 330-613.

Silveira, F.A. 1993. Phylogenetic relationships of the Exomalopsini and Ancylini (Hymenoptera: Apidae).The University of Kansas Science Bulletin 55:163-173.

Silveira, F.A. 1995. Phylogenetic Relationships and Classification of Exomalopsini (Insecta:Apidae), with a Revision of the *Exomalopsis (Phanomalopsis) jenseni* Species-group and a Catalog of the Species of Exomalopsini. Lawrence, The University of Kansas, vii +168pp. Dissertation.

Silveira, F.A., L.B. Rocha, J.R. Cure, M.J.F. Oliveira. 1993. Abelhas silvestres (Hymenoptera, Apoidea) da Zona da Mata de Minas Gerais. II – Diversidade, abundância e fontes de alimento em uma pastagem abandonada em Ponte Nova. Revista Brasileira de Entomologia 37:595-610.

Smith, F. 1854.Catalogue of Hymenopterous Insects in the Collection of the British Museum. Part II. Apidae. London, British Museum. 465pp.

Smith, F. 1879. Descriptions of New Species of Hymenoptera in the Collection of the British Museum. London, 240pp.

Spinola, M. 1853. Compte rendu des hyménoptères inédits provenants du voyage entomologique de M.Ghiliani dans le Para en 1846. Memorie della Reale Accademia delle Scienze di Torino (2)13:19-94.

Taschenberg, E. 1883. Die Gattungen der Bienen (Anthophila). Berliner Entomologische Zeitschrift 27:37-100.

Timberlake, P.H. 1947. A revision of the species of *Exomalopsis* inhabiting the United States (Hymenoptera, Apoidea). Journal of the New York Entomological Society 55:85-106.

Timberlake, P.H. 1980. Review of North American *Exomalopsis*. University of California Publications on Entomology 86:1-158.

Toro, H. 1976. *Chilimalopsis*, nuevo genero chileno de Exomalopsini (Hymenoptera = Apoidea). Anales del Museo de Historia Natural de Valparaiso 9:73-76.

Wiley, E.O., D. Siegel-Causey; D.R. Brooks, V.A. Funk. 1991. The Compleat Cladist. A Primer of Phylogenetic Procedures. The University of Kansas Museum of Natural History Special Publication no.19. Lawrence, The University of Kansas, x + 158pp.

Zucchi, R. 1973. Aspectos Bionômicos de *Exomalopsis aureopilosa* e *Bombus atratus*, Incluindo Considerações sobre a Evolução do Comportamento Social (Hymenoptera – Apoidea). Ribeirão Preto, Faculdade de Filosofia Ciências e Letras de Ribeirão Preto, vii + 172pp. Thesis.

ANNOUNCEMENT

The *University of Kansas Science Bulletin* (continuation of the *Kansas University Quarterly*) is an outlet for scholarly scientific investigations carried out at the University of Kansas or by University faculty and students. Since its inception, volumes of the *Bulletin* have been variously issued as single bound volumes, as two or three multi-paper parts or as series of individual papers. Issuance is at irregular intervals, with each volume prior to volume 50 approximately 1000 pages in length. Effective with volume 50, page size has been enlarged, reducing the length of each volume to about 750 pages.

The supply of all volumes of the *Kansas University Quarterly* is now exhausted. However, most volumes of the *University of Kansas Science Bulletin* are still available and are offered, in exchange for similar publications, to learned societies, colleges and universities and other institutions, or may be purchased at $30.00 per volume. Where some of these volumes were issued in parts, individual parts are priced at the rate of 3 cents per page. Current policy, initiated with volume 46, is to issue individual papers as published. Such separata may be purchased individually at the rate of 7 cents per page, with a minimum charge of $1.50 per separate. Subscriptions for forthcoming volumes may be entered at the rate of $30.00 per volume. All communications regarding exchanges, sales and subscriptions should be addressed to the EXCHANGE LIBRARIAN, UNIVERSITY OF KANSAS LIBRARIES, LAWRENCE, KANSAS 66045.

Reprints of individual papers for personal use by investigators are available for most recent and many older issues of the *Bulletin*. Such requests should be directed to the author.

The International Standard Serial Number of this publication is US ISSN 0022-8850.

Editor
Charles D. Michener

Editorial Board
Meredith Lane, *Chairman*
James S. Ashe
George W. Byers
Christopher Haufler
Norman A. Slade

THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. 55, No. 13, pp. 455-518 November 10, 1995

DEC 18 1995

Revision of the Neotropical Termite Genus *Syntermes* Holmgren (Isoptera: Termitidae)[1]

Reginaldo Constantino[2]

TABLE OF CONTENTS

Abstract 455
Introduction 456
Acknowledgments 456
Biology and ecology of *Syntermes* 456
Formation of sterile castes, 456; Nesting behavior, 457; Feeding habits, 459; Termitophiles and inquilines, 460; Fossil record, 460; Economic importance, 460.
Material and methods 462
Key to the imagoes of *Syntermes* 462
Key to the soldiers of *Syntermes* 463
Taxonomy 465
Phylogenetic relations of the species of *Syntermes* 506
Literature cited 516

ABSTRACT

The taxonomy of the genus *Syntermes* is revised, and 23 species are now recognized. Six species are described as new: *S. barbatus*, *S. cearensis*, *S. crassilabrum*, *S. longiceps*, *S. nanus*, and *S. tanygnathus*; the imagoes of *S. aculeosus*, *S. chaquimayensis*, and *S. wheeleri* are described for the first time; two species are revalidated: *S. bolivianus* and *S. wheeleri*; and six new synonymies are proposed: *S. hageni* (previously treated as a synonym of *S. dirus*) and *S. lighti* are junior synonyms of *S. grandis*, and *S. solidus*, *S. chaquimayensis parvinasus*, *S. emersoni*, and *S. robustus* are junior synonyms of *S. spinosus*. Drawings of imagoes, soldiers and workers, as well as distribution maps are presented for all species, except the imagoes of six species, which are still unknown. Keys for the identification of both imagoes and soldiers of *Syntermes* are presented. A phylogenetic analysis of the species of *Syntermes* was made based on 21 soldier characters, 10 imago characters, 12 worker characters (mandibles and digestive tube), nest type and habitat. Several groups of species are well supported, but the mid-level branching of the tree is poorly resolved. The large size and the thoracic spines of the soldiers of *Syntermes*, usually considered as a primitive condition, appear as derived characters in this analysis.

[1] Contribution number 3153 from the Department of Entomology, University of Kansas. This paper is part of a dissertation presented to the University of Kansas in partial fulfillment of the requirements for a Ph.D. degree.

[2] Snow Entomological Museum, Snow Hall, University of Kansas, Lawrence, KS 66045, U.S.A.

INTRODUCTION

The neotropical genus *Syntermes* is restricted to the forests and savannas of South America east of the Andes, from Venezuela to northern Argentina, and comprises some of the largest termites in the world. As far as their biology is known, most species live in subterranean nests and feed on leaf- or grass-litter, and a few have been recorded as pests in agriculture and forestry.

Their large size has attracted the attention of general collectors but their subterranean habits and their tendency to hide quickly underground when disturbed have resulted in meager collections. Beginning with Latreille's (1804) *Termes spinosum*, several species now assigned to *Syntermes* were originally described in the genus *Termes*. (At the time of those descriptions, *Termes* was almost synonymous with our current Order Isoptera). Early in this century, Holmgren (1910) proposed a new classification for the order Isoptera, including the new genus *Syntermes* in the subfamily Termitinae of the Metatermitidae, and designating *Termes dirus* as its type-species. Subsequently, Holmgren (1911) presented a list and a key for the identification of the nine species included in *Syntermes*, five of them new and four transferred from *Termes*. A description of the genus was given in Holmgren's (1912) monograph on family Metatermitidae, including a discussion about its phylogenetic relations and new subdivision of that family. *Syntermes* was then included in a group named "*Syntermes*-Reihe", which is synonymous with the current concept of the subfamily Nasutitermitinae. Later, Snyder (1924) presented a new taxonomic account of *Syntermes*, including a new key and the description of four new species.

Based on admittedly limited material, Emerson (1945) revised the taxonomy of *Syntermes*, recognizing 18 species, one of them divided into three subspecies. In a brief discussion about the phylogenetic relations of *Syntermes*, Emerson (1945: 441) states that it is the most primitive genus of the Nasutitermitinae and that it is somehow related to the genus *Acanthotermes* in Macrotermitinae. His argument in favor of the primitiveness of *Syntermes* was based on the presence of many characters believed to be primitive.

After Emerson's revision, Silvestri (1946) described two new species, and Araujo (1977) placed four names in synonymy, based on his own observations and on information provided by A.E. Emerson. More recently, thanks to the efforts of many termitologists and collectors, a large amount of new material of *Syntermes* has been made available for study, including several undescribed species and castes and new data on the geographical distribution and morphological variation of most species.

Syntermes is currently included in the subfamily Nasutitermitinae, and clearly belongs to a group of 13 neotropical genera usually called the mandibulate nasutes, due to the fact that their soldiers bear both a frontal tube (sometimes very short) and functional mandibles, in contrast with the true nasutes, which have very long frontal tubes and vestigial mandibles. However, the traditional hypothesis that the mandibulate nasutes are the basal lineages of the Nasutitermitinae is not well supported by a formal cladistic analysis (Constantino, in prep.), and it is possible that the presence of a frontal tube in both groups is a case of convergence or parallelism. This question is currently being examined by the author, and changes in the classification might be proposed in the near future.

In the revision below, I present a review of the literature on *Syntermes*, new keys for the identification of imagoes and soldiers, a description of each species, including six new ones, new synonymies, the revalidation of two names previously treated as synonyms, and an analysis of the phylogenetic relations among the species.

ACKNOWLEDGMENTS

During the course of this work the author was supported by a scholarship from the Conselho Nacional de Desenvolvimento Científico e Tecnológico, Brazil (No. 200809/91-1). Visits to the American Museum of Natural History, U.S. National Museum of Natural History, and Museum of Comparative Zoology were supported by grants from those institutions. This work would not be possible without the material sent for study by many institutions and colleagues, in special E.M. Cancello (MZSP), R.T. Shuh (AMNH), The Natural History Museum, London, M.S. Collins (USNM), and A.G. Bandeira (INPA) (complete list of institutions presented in the methods section). O.F. Souza, G.R. Colli, and K. Kitayama provided invaluable support during my field trip to Brazil. I thank Ch. Noirot for sending information on the formation of sterile castes of *Syntermes*. I am also grateful to Byron Alexander for helpful discussions and a careful revision of the manuscript.

BIOLOGY AND ECOLOGY OF *SYNTERMES*

Formation of sterile castes

Since the taxonomy of termites is heavily based on the morphology of sterile castes, it is important to understand their polymorphism and how they develop. In the case of *Syntermes*, this has never been fully studied, and we have to rely on fragmentary information in the literature and on the analysis of preserved material. The only published data about the formation of castes in *Syntermes* are those presented by Noirot (1969: 329) based on his analysis of *S. wheeleri*. A diagram of the most probable pathway of development of workers and soldiers is presented in Fig. 1.

The worker caste of *Syntermes* has always been described as dimorphic. Nevertheless, careful examination of large samples clearly shows that there are four different workers: two less sclerotized with white heads of different sizes; and two more sclerotized ones with yellow to yellow-brown heads. The white-head workers are females and the dark-head workers are males, both found in two sizes corresponding to third and fourth instars. The 3rd instar male worker is about the same size as the 4th instar female worker. The 4th instar male worker is much larger than the others and is also the type most commonly found in collections.

The soldier caste of *Syntermes* probably develops from the large male worker, which molts and becomes a presoldier and then a soldier. It is believed to be monomorphic but, among the material examined in the course of the cur-

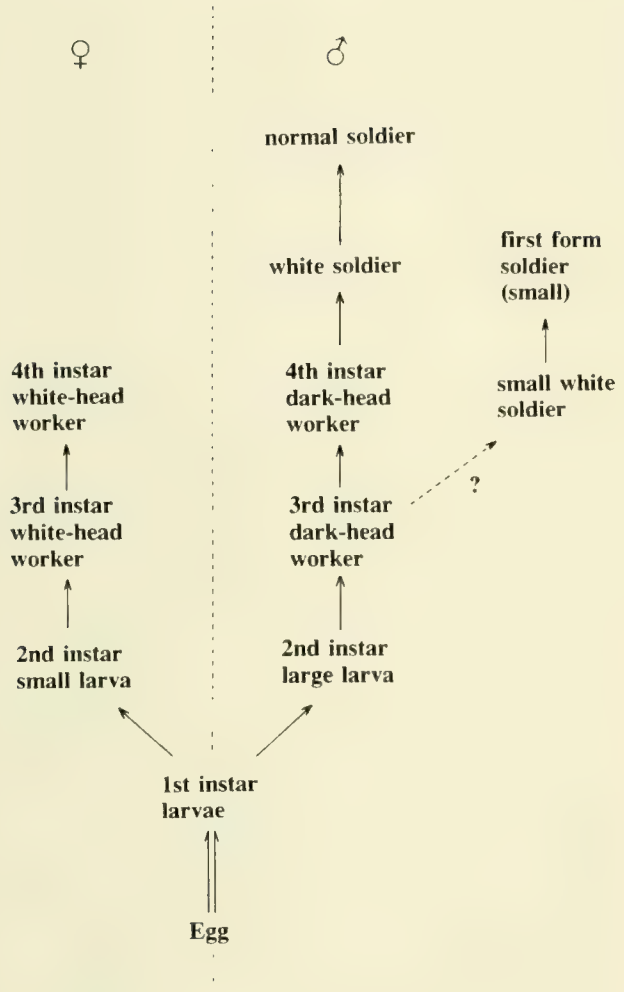


Fig. 1. Most likely developmental pathways of the sterile castes of *Syntermes*. Modified from Noirot (1969: 329 and personal communication), and Silvestri (1946).

rent revision, there are a few samples with two sizes of soldiers. The most probable explanation for this occurrence was presented by Silvestri (1946), based on his observations on *S. praecellens*. Young colonies of that species produce soldiers considerably smaller than and morphologically distinct from soldiers in older colonies. Silvestri called these smaller soldiers "forma prima" (first form), contrasting with "forma perfecta" (perfect form) soldiers. This phenomenon has also been observed in other genera of Termitidae (Noirot, 1969). In most cases the pathway of development is the same and the soldiers are just smaller than normal, but in some species (e.g., *Pericapritermes urgens*), the first soldiers develop from an earlier instar and are morphologically very distinct. In the case of *Syntermes*, my hypothesis is that in young colonies soldiers develop from the 3rd instar male worker instead of the 4th instar and in intermediate stages both kinds of soldiers could be found in the colony, which would explain the few samples with two sizes of soldiers. As Silvestri (1946) already warned, this phenomenon is very important for taxonomy because a first form soldier could be taken as a species distinct from the normal soldier.

A relatively common phenomenon is the presence of individuals intermediate between workers and soldiers. These intercastes were first reported by Silvestri (1945a) for *S. grandis* and, according to his detailed study, are caused by a microsporid protozoan. They can easily be identified by the presence of numerous white cysts in the abdomen.

Nesting behavior

Termite nests are sometimes extremely complex structures, which can be a good source of information for taxonomic and phylogenetic studies. The nests of most species of *Syntermes* have never been adequately described in the literature (Noirot 1970: 80), probably because in most cases they are subterranean and difficult to study. Based on the descriptions available in the literature and on my own observations of several species, the nests of *Syntermes* can be divided into three main types: completely subterranean; subterranean with a pile of loose soil on the surface; and compact mound.

Fig. 2. Nest of *Syntermes dirus* from the Brazilian Atlantic forest. Above-ground portion is soft.

Several species seem to live in completely subterranean nests, and those are the most difficult to collect and to study. Some of the more common species, such as *S. molestus* and *S. nanus*, and most of the little-known species, have this type of nest. The only detailed description of a subterranean nest was that by Silvestri (1946), who discovered by chance an exposed nest of *S. praecellens* in a construction site in the city of São Paulo. The central portion (endoecie) of that nest was found at a depth of three meters, was approximately spherical and had a diameter of about 45 cm (Fig. 4). It was composed of many thin horizontal chambers divided by vertical walls, and had a fragile structure. Silvestri also mentions that workers collect plant material on the surface and store it in subterranean chambers. The nests of *S. molestus* and *S. nanus* are certainly subterranean, but an endoecie was never found, probably because it is located deep in the soil as in *S. praecellens*, and extremely difficult to find. Darlington (1993) briefly described the subterranean galleries and storage chambers of a nest attributed to *S. molestus* (probably *S. nanus*, because it was found in cerrado vegetation). The galleries were about one centimeter in diameter and were covered with a weak lining of cemented soil particles. The storage chambers were 7-10 cm long and 1 cm high, irregularly shaped.

In his monograph on termite nests, Emerson (1938) described the nest of *Syntermes spinosus* (as *S. snyderi*), studied by himself in Guyana, as "simple excavations in the sandy-clay soil", with a pile of "excavated dirt" on the surface, and also mentioned that leaf fragments were stored in some compartments of the nest. Emerson considered the nest of *Syntermes* as primitive and used it as evidence for the primitiveness of the genus. Holmgren's (1906: 662) description of the nest of *S. chaquimayensis* seems to have been overlooked by later authors, including Emerson. According to Holmgren's description, the nest of that species is found only in rain-forest, commonly at the base of a palm or other tree, making it very difficult to study because of the presence of many roots. It also has a pile of loose soil on the surface with sparse cylindrical galleries, and a vast subterranean part with many large, flat chambers, in which he found larvae and stored plant material. He did not find the bottom of this part after having excavated to a depth of more than a meter. Like *S. spinosus* and *S. chaquimayensis*, *S. dirus* is a forest species and builds a semi-subterranean nest with a large

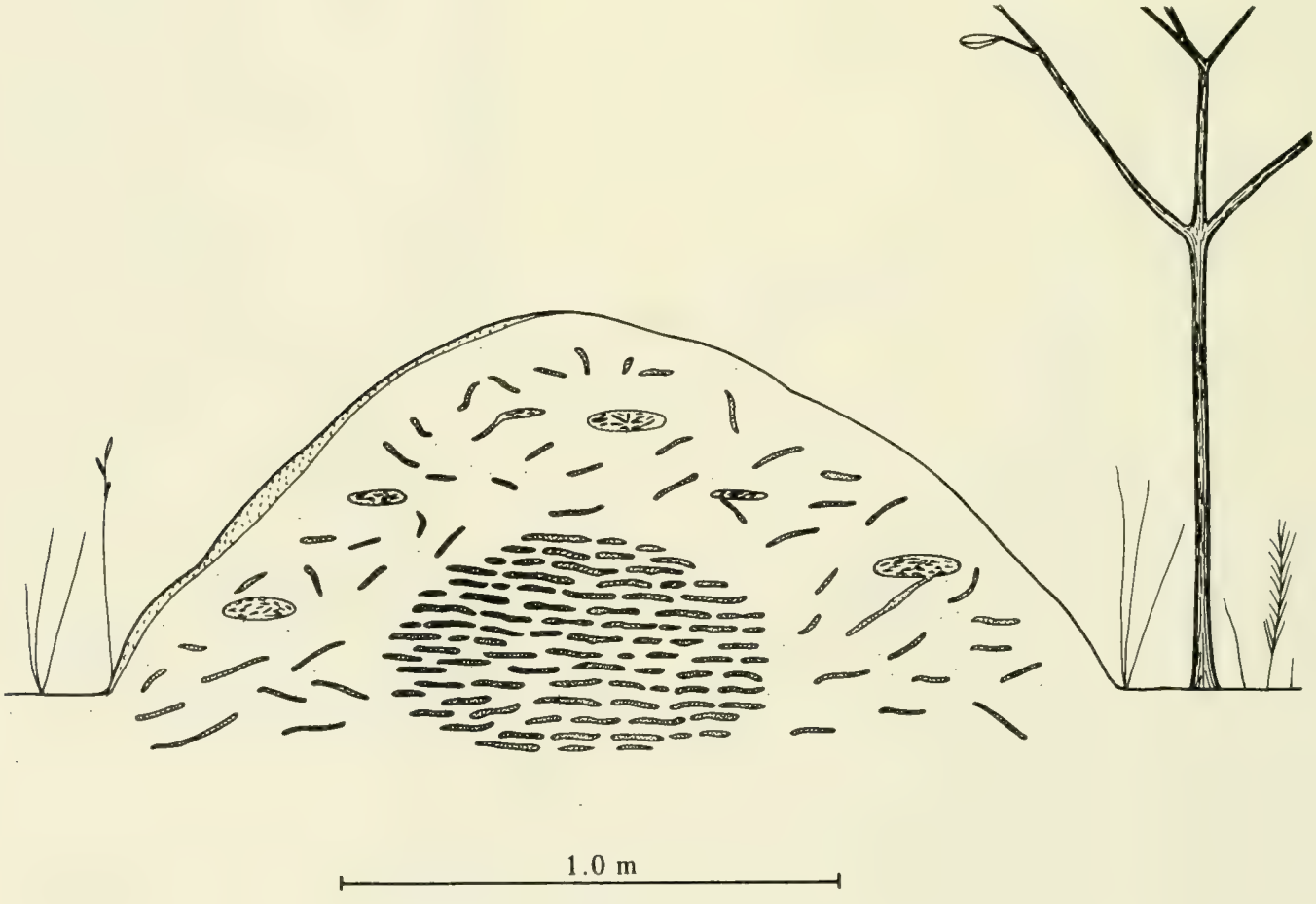


Fig. 3. Nest of *Syntermes wheeleri* from the cerrado vegetation of Central Brazil. Above-ground portion is hard.

pile of loose soil on the surface (Fig. 2). However, based on my observations, there is a clearly differentiated central portion below ground with many horizontal, thin chambers. The chamber walls are fragile and brittle, and have a color and consistency distincly different from the surrounding soil, indicating that this part of the nest was constructed and not simply excavated. The pile of loose soil above ground lacks any internal structure, but has several galleries lined with pelleted soil and some chambers with stored leaf litter.

Holmgren (1906: 661) also presented a detailed description of the nest of *S. peruanus* (misidentified as *T. dirus*), which also has been overlooked. He described the nest of that species as a complex structure, with a true, above-ground, compact mound about 50 cm in height and 2 m or more in diameter, found only in dry areas without trees. Holmgren divided that nest into three parts: a thin external layer with few galleries; a thick layer with numerous galleries and rounded chambers between the first layer and the soil surface; and a subterranean part with many flat and wide chambers. There is no differentiated royal cell and the queen or queens live in any chamber in the subterranean portion. Larvae and stored grass are also found in this subterranean portion. Grass is stored mainly in a concave layer of chambers at the bottom of the nest. Negret & Redford (1982: 90), briefly described the nests of *S. wheeleri* (misidentified as *S. dirus*) from the cerrado of Central Brazil as "low-domed termitaria, the major part of which are below ground level (often to a depth of 1.5 m). The galleries are large and diffuse, often containing grass stores and are lined with regurgitated soil in which individual pellets are clearly visible." However, according to my own observations of the nest of *S. wheeleri* in Central Brazil, its structure appears similar to the nest of *S. peruanus* and can be divided into three distinct parts (Fig. 3): an external, hard, thin layer without galleries; a thick layer with many galleries and storage chambers; and a central part (endoecie) with many flat, wide and thin chambers with fragile walls, which are not lined with soil pellets but have a smooth surface. Some larvae were found in this central part, but the termites, including the queen, seem to be able to escape quickly through the wide galleries. No differentiated royal chamber was found, but there is enough space for the queen in all chambers and galleries.

The nest of *S. grandis*, from the cerrado of Central Brazil and other savannas, seems to be intermediate between the mound type and the loose soil type (Coles, 1980: 51, and my own observations). It is mostly subterranean but has a small, flat mound of soft consistency above ground. No description of the subterranean part is available.

A photograph of a spherical subterranean termite nest attributed to a *Syntermes* species was published by Snyder (1948: 79). That photograph was taken during a study conducted by Fonseca (1949, Fig. F), who clearly states that the spherical nest did not belong to a *Syntermes* species, although some less conspicuous galleries and chambers made by *S. molestus* can be seen in the same picture. It is important to make this correction because Noirot (1970: 80), based on that picture, suggests that the nests of *Syntermes* may have a paraecie, which is not true.

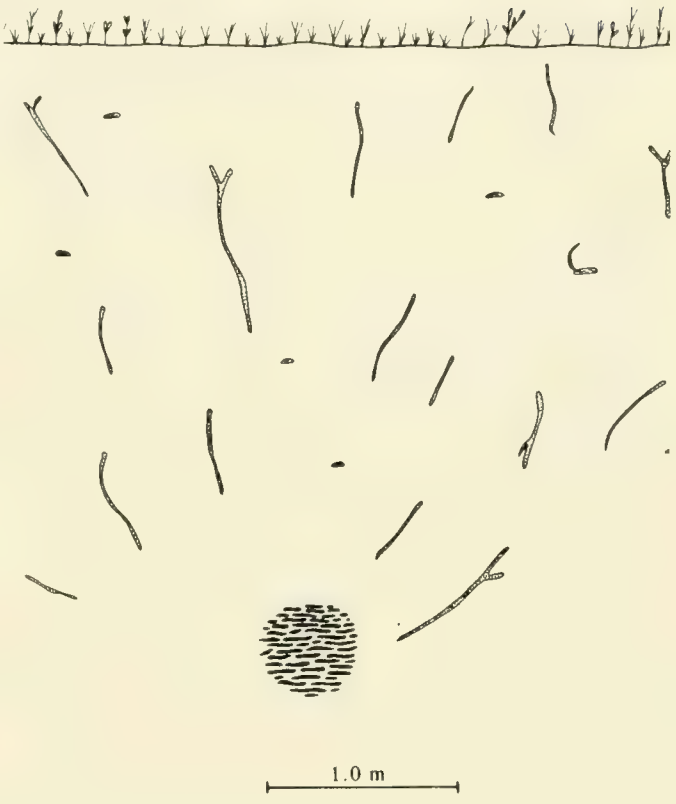


Fig. 4. Nest of *Syntermes praecellens*. After Silvestri (1946).

The nests of many species of *Syntermes* still remain completely unknown. However, based on the information available, it appears that the presence of a central portion with many thin, flat and wide chambers, as well as an extensive system of subterranean galleries with storage chambers, is characteristic and can possibly be considered a synapomorphy of the genus. Other related genera, such as *Cornitermes*, *Labiotermes* and *Procornitermes*, have different types of nest, with a predominance of smaller, globular cells. None of these genera is known to store plant material inside the nests.

Feeding habits

All species of *Syntermes* seem to be specialized feeders on leaf- or grass-litter, which they collect above ground in the open and store in subterranean chambers. This is supported by the facts that grass or leaf stores have been consistently found inside their nests and that the following species have been observed foraging: *S. molestus* (as *S. brasiliensis*) and *S. grandis* (Bequaert, 1925); *S. praecellens* (Silvestri, 1946); *S. wheeleri* (misidentified as *S. dirus*), *S. gran-*

dirus, *S. nanus* sp.n. (misidentified as *S. molestus*), and *S. barbatus* sp.n. (misidentified as *S. brevimalatus*) (Coles, 1980; Negret & Redford, 1982); *S. spinosus* (misidentified as *S. chaquimayensis*), *S. molestus* and *S. parallelus* (Bandeira, 1991; Barbosa, 1993).

Savanna species feed mostly or exclusively on grasses. They forage in the open at night and at dusk, leaving their nest from small exit holes and forming a foraging line of workers guarded by soldiers. Workers cut grass, both living and dead, into pieces, sometimes climbing up grass tussocks, and carry them to their nest. Apparently they never consume grass above ground.

Forest species forage in a similar manner, but they seem to eat only leaf litter, which they cut into circular pieces and carry to their nest. According to Barbosa (1993), *S. spinosus* and *S. molestus* forage mainly between 7 P.M. and 3 A.M. in a forest in Central Amazonia. However, some forest species have been seen foraging during the day, and I had the opportunity to observe *S. molestus* foraging around 11 A.M. in an eastern Amazonian forest.

Apparently no one has ever tried to estimate the contribution of the activities of *Syntermes* species to total litter decomposition. Luizão & Schubart (1987) estimated that termites in general are responsible for a litter weight loss of 40% or more during the wet season in some forests in Central Amazonia, referring to *Syntermes* species as the most important members of the litter-feeding termite assemblage.

Termitophiles and inquilines

Due to the subterranean habits of most *Syntermes* species, the study of termitophiles associated with them has been greatly limited. The list in Table 1 was based on the following references: Wasmann (1894), Borgmeier (1930, 1935, 1959), Reichensperger (1936), Seevers (1941, 1957), Silvestri (1945b), Dybas (1955). The identification of the host species was corrected when possible. Species marked with an asterisk were considered as probably not true termitophiles by Seevers (1957).

A termitolestic ant of the genus *Carebara* was collected by Emerson in a nest of *Syntermes spinosus*, and described by Wheeler (1922). Both Wheeler (1936: 199) and Emerson (1945: 436) considered this finding important evidence for the relationship between *Syntermes* and the macrotermitine genera *Acanthotermes*, *Macrotermes*, and *Odonthotermes*, because *Carebara* is otherwise found only associated with the mounds of these genera. However, there are no additional records of those ants associated with *Syntermes*, and this termitolestic association is only hypothetical. The putative phylogenetic relationship between *Syntermes* and those African macrotermitine genera is not supported by a strict cladistic analysis, and if there is any association between *Carebara* and *Syntermes* species, this is probably due to ecological similarities involving nesting and feeding behavior.

Several species of termites are also frequently associated with the nests of *Syntermes*. These are usually called inquilines by termitologists, but the nature of their association is unknown. These termites are probably associated with the nest itself instead of the species that builds it, since they live in separate galleries and possibly never meet their hosts, except for some accidental encounters. In some *Cornitermes* species, it is common to find more than 10 inquiline species in a single nest (Mathews, 1977). The figures are not so impressive in *Syntermes*, and usually no more than two to five inquiline species are found in a single nest. The following list was based on collectors' notes and on my own observations. Data are available for only three species, probably because they are relatively common and build conspicuous nests.

S. dirus: *Heterotermes* sp; *Anoplotermes* sp; *Neocapritermes* sp; *Orthognathotermes* sp; *Spinitermes* sp; *Procornitermes lespesii*; *Subulitermes* sp.

S. grandis: *Anoplotermes* sp; *Orthognathotermes* sp; *Subulitermes microsoma*.

S. wheeleri: *Anoplotermes* sp; *Dentispicotermes* sp; *Dihoplotermes* sp; *Spinitermes* sp; *Paracornitermes* sp.

Fossil Record

There is no positive record of any fossil *Syntermes*, but Bown & Laza (1990) described a Miocene fossil termite nest from southern Argentina which they attributed to a *Syntermes* species. However, based on their description and illustrations, I do not see any positive evidence that what they found was even a termite nest, and it does not look like any known nest of *Syntermes*. Given the facts that the descriptions of *Syntermes* nests in the literature are very poor and that those authors based their analysis on published information only, their identification should be considered doubtful.

Economic importance

There are a few records of *Syntermes* species causing damage to cultivated plants, including young *Eucalyptus* trees (Fonseca, 1949), peanuts (Cruz et al., 1962), rice (Ramalho, 1976), pastures (Mariconi et al., 1976), sugar-cane (Guagliumi, 1971; Mendonça-Filho, 1972) and yams (Veiga, 1974). Most cases of damage seem to be associated with the period immediately after the conversion of natural habitats into cultivated land, when the termites, deprived of their natural food, will eat any plant material available. There are no published estimates of the economic losses and control expenses involved. Fonseca (1949) reports that *S. nanus* (as *S. molestus*) and *S. insidians* can cause considerable damage to young *Eucalyptus* trees in some areas, destroying up to 70% of them.

Several species of *Syntermes* have been reported as being used as food by native peoples of South America. Weidner (1980) mentions that soldiers and workers of *S. aculeosus* are consumed by Indians in southern Colombia. According to Dufour (1987), alates and soldiers of *Syntermes* are an important food item for the Tukanoan Indians in the Colombian Amazon. Soldiers are consumed during ritually restricted diets in which ant and termite soldiers are the only animal food permitted. One sample of *S. aculeosus* from Venezuelan Amazon has the following label information:

TABLE 1. List of termitophiles associated with *Syntermes* species.

Termitophile	Hosts
THYSANURA: Lepismatidae	
Grassiela praestans Silvestri	*S. dirus*; also *Cornitermes*, *Nasutitermes*, *Spinitermes*, *Anoplotermes*, *Embiratermes*
Gastrotheus synterminus Silvestri	*S. dirus*
COLEOPTERA: Staphylinidae	
Aleocharinae	
Chaetonannus fragilicornis Borgmeier	? *S. molestus*
Termitonannus validus Silvestri	*S. wheeleri*
Termitopelta fulgens Borgmeier	*S. molestus*
Termitophagus synterminus Silvestri	*S. wheeleri*
Iheringocantharus ypiranganus Bernhauer	*S. wheeleri*
Atheta convivens Silvestri *	*S. wheeleri*
Atheta syntermitis Silvestri *	*S. wheeleri*
Atheta silvestrii Seevers *	*Syntermes* sp; also *Anoplotermes*
Atheta termitobia Wasmann *	*S. dirus*
Staphylininae	
Belonuchus penetrans Silvestri *	*S. obtusus*
Paederinae	
Termitosaurus insinuatus Silvestri *	*S. wheeleri*
Tachyporinae	
Termitoplus grandis Silvestri	*S. wheeleri*; *S. obtusus*
COLEOPTERA: Ptiliidae	
Urotriainus grandis Silvestri	*S. wheeleri*
Urotriainus grandis var. *robustior* Silvestri	*S. dirus*
Urotriainus molesti Silvestri	*S. molestus*
Pycnopteryx schmidti Dybas	*S. molestus*
Pycnopteryx sp.	*S. spinosus*
COLEOPTERA: Histeridae	
Cossyphodister schwarzmaieri Reichensperger	*Syntermes* sp.
Scapolistes sternalis Borgmeier	*S. molestus*
COLEOPTERA: Scarabaeidae	
Acanthocerus termiticola Wasmann	*S. dirus*
DIPTERA: Phoridae	
Cryptophora coeca Borgmeier	*S. molestus*
Cryptophora colombicae Seevers	*S. molestus*
Syntermophora microphtalma Seevers	*S. molestus*

* Considered as probably not true termitophiles by Seevers (1957).

"Indians bite off head and eat them; grind heads and mix with salt or oil and refrigerate; aphrodisiac or taste enhancer in cooking — hot and spicy like pepper." A vial with salted, pulverized soldier heads prepared by those Indians came with that sample and it tastes really hot. The spicy taste comes from the defensive secretions from the frontal gland, which have not been studied in *S. aculeosus*. In other species of *Syntermes* this gland contains a mixture of mono- and sesquiterpene hydrocarbons (Baker et al., 1981). Tukanoan Indians in the Brazilian Amazon, close to the Colombian

border, use *Syntermes tanygnathus* sp.n. (and probably other species as well) as a spice, cooking whole soldiers together with fish (R.B. Barthem, personal communication). Termite alates in general are known to be part of the diet of many groups of South American Indians and *Syntermes* species, due to their large size, are probably an important component.

MATERIAL AND METHODS

About 700 samples (vials) in alcohol and a few pinned specimens were examined, from the following entomological collections: American Museum of Natural History, New York (AMNH); Università degli Studi di Napoli, Departamento di Entomologia e Zoologia agraria (Silvestri's collection), Portici, Italy (LEFS); Institut Royal des Sciences Naturelles de Belgique, Brussels (ISNB); Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil (INPA); Museu Paraense Emílio Goeldi, Belém, Brazil (MPEG); Museu de Zoologia da Universidade de São Paulo, Brazil (MZSP); Museum of Comparative Zoology, Harvard University (MCZ); Museum National d'Histoire Naturelle, Paris (MNHN); Museum für Naturkunde, Humboldt Universität, Berlin (ZMHU); The Natural History Museum, London (BMNH); Naturhistoriska Riksmuseet, Stockholm (NHRS); Universidad Nacional del Nordeste, Corrientes, Argentina (UNN); Universidade de Brasília, Brazil (UnB); Universidade Federal de Goiás, Goiânia, Brazil (UFG); Universidade Federal de Viçosa, Brazil (MEUV); Zoological Museum, University of Copenhagen (ZMUC); U.S. National Museum of Natural History, Washington, D.C. (USNM).

The terminology used for imago and worker mandibles is the same as that used by Krishna (1968: 265) and Fontes (1987: 504), and is indicated in Fig. 13. Both mandibles have an apical tooth (A) and two marginal teeth. On the left mandible, the first marginal tooth is considered to be a fusion of two teeth found in other taxa and is called first plus second marginal tooth (M_{1+2}), and, consequently, the second one is referred to as the third marginal tooth (M_3). On the proximal part of the left mandible there is a molar prominence (MPr) with ridges on its crushing surface. Under the molar prominence there is another tooth, named the molar tooth (Mt, indicated in Fig. 14). On the right mandible, the marginal teeth are named first marginal (M_1) and second marginal (M_2), and on its proximal inner part there is a molar plate (MP), which also has ridges on its crushing surface. On the proximal part of the molar plate there is a notch, named the basal notch (BN). Since soldier mandibles are derived from worker mandibles, their dentition is homologous and I use the same terminology, except for the marginal teeth of the left mandible, which I prefer to designate M_1 and M_2 (Fig. 58).

Terms used for the digestive tube are the same as those used by Noirot & Noirtot-Timothée (1969), indicated in Figs. 28-34. Most terms used for external morphology are of common use in entomology and do not need any special explanation, with the exception of the frontal tube of the soldier and the fontanelle. The frontal tube, also called the nasus, is present only in the soldier caste of some groups of termites. It has a pore at its tip, which is connected to a reservoir of a defensive secretion inside the head. The term fontanelle has been used with two different meanings in the termite literature (Weesner, 1969). In taxonomy it has been used to refer to an area of reduced sclerotization present on the top of the head of imagoes and workers of some taxa, which is associated with a pore, also called the fontanelle. I am here using the term fontanelle to refer to the area of reduced sclerotization, and the pore itself is not mentioned in the descriptions. Terms used for hair-like structures are comparative. Bristles are long, with well-marked bases, and found on the head, thoracic nota, posterior margins of tergites and sternites, and legs. Hairs are thinner and less conspicuous. Tibial spurs are thick and present on the apical part of the tibiae.

Drawings were prepared using a camera lucida coupled with a dissection microscope. Measurements were taken with a micrometric reticle on the eyepiece of the dissection microscope. Most measurements were explained and illustrated by Roonwal's (1970), and correspondence to his system is indicated by the numbers in brackets. Measurements without any equivalent in Roonwal's system are explained.

1. length of head to lateral base of mandibles, taken laterally [5].
2. maximum width of head excluding eyes, taken dorsally [17].
3. minimum width of head, at the base of the mandibles, taken dorsally [19].
4. height of head excluding postmentum, taken laterally [21].
5. length of fontanelle: length of the area of reduced sclerotization present on the top of head of imagoes and workers, taken dorsally.
6. maximum diameter of eye, taken laterally [48]
7. maximum diameter of ocellus, taken dorsally [55]
8. length of forewing from basal suture [74]
9. maximum width of forewing.
10. maximum length of pronotum, taken dorsally [65]
11. length of frontal tube: distance between the tip and the base of the frontal tube present on the top of the head of soldiers, taken laterally.
12. length of left mandible, taken dorsally [37]
13. curvature of the left soldier mandible: the distance between the tip of the mandible and a line tangential to its outer margin, taken dorsally (indicated in Fig. 23).
14. distance M_1-M_2 on left mandible: distance between the tips of the two marginal teeth of left soldier mandible, taken ventrally (Fig. 23).
15. width of left mandible: minimum distance between the outer and inner margin of the soldier mandible between M1 and M2, taken ventrally (Fig. 23).
16. length of left M1: distance between the tip of the first marginal tooth and the apical cutting edge of left soldier mandible, taken ventrally (Fig. 23).
17. minimum width of postmentum [63]
18. maximum width of pronotum, including spines [68]
19. maximum width of metanotum, including spines [72]
20. length of hind tibia [85]

KEY TO THE IMAGOES OF *SYNTERMES*

Note: Alates are difficult to identify and in some cases those of two different species are indistinguishable. It is important to keep in mind that the alates of several species are still unknown, and that the descriptions and the key below are, in most cases, based on limited material. Some species may show more variation than is currently known. Correct identification depends on careful comparison of descriptions, geographical distribution, and habitat. Care should also be taken with broken antennae and missing hairs, which can be easily rubbed off from the top of the head and other areas.

1. Head capsule in dorsal view[3] with fewer than 20 hairs posterior to clypeus (Fig. 59); eyes small, less than 0.26 width of head; wings brown 2
Head capsule in dorsal view with more than 30 hairs posterior to clypeus (Fig. 198); eyes and wings variable 8

2(1). Width of pronotum more than 3.5mm; postclypeus with 6 or more hairs 3
Width of pronotum less than 3.5mm; postclypeus with 2 or 4 hairs 6

3(2). Antenna with 21 articles; Colombian Amazon and westernmost Brazilian Amazon (Figs. 285-287) .....*S. tanygnathus*
Antenna with 19-20 articles (3rd article sometimes partially subdivided) 4

4(3). Anterior margin of postclypeus with 6 long hairs; top of head with conspicuous, fairly long hairs; widely distributed in Amazonia and Mato Grosso (Figs. 274-276) .....*S. spinosus*
Anterior margin of postclypeus with 2-4 hairs; hairs on top of head short and inconspicuous, sometimes barely visible 5

5(4). Ratio of length to width of pronotum less than 0.5; length of fontanelle 0.47-0.57mm; western and northern Amazonia (Figs. 59-61) .....*S. aculeosus*
Ratio of length to width of pronotum more than 0.5; length of fontanelle 0.3-0.5mm; eastern Amazonia to Brazilian Atlantic forest (Figs. 131-133) .....*S. dirus* or *S. cearensis*[4]

6(2). Anterior corners of pronotum nearly rounded; postclypeus with 4 hairs (Figs. 296-298) ..*S. territus*
Anterior corners of pronotum distinctly angular (Figs. 178, 238); postclypeus with only two hairs on anterior margin (Figs. 176, 236) 7

7(6). Ratio of length of hind tibia to width of head without eyes less than 1.8; central and eastern Amazonia (Figs. 176-178) .....*S. longiceps*
Ratio of length of hind tibia to width of head without eyes more than 1.8; northern Amazonia and Guianas (Figs. 236-238) .....*S. parallelus*

8(1). Width of head without eyes less than 2.8mm; anterior corners of pronotum rounded (Figs. 200, 211) 9
Width of head without eyes more than 2.8mm; anterior corners of pronotum slightly to strongly angular (Figs. 109, 149, 257) 10

9(8). Width of pronotum less than 2.7mm; ratio diameter of eye to width of head 0.32-0.38mm; length of fontanelle 0.17-0.34; head and pronotum dark brown; fontanelle about the same color as head capsule or a little paler; cerrado vegetation (Figs. 209-211) .....*S. nanus*
Width of pronotum more than 2.7mm; ratio diameter of eye to width of head 0.28-32mm; length of fontanelle 0.34-0.45; head and pronotum chestnut brown; color of fontanelle conspicuously paler than head capsule; from Amazonia to Brazilian Atlantic forest (Figs. 198-200) *S. molestus*

10(8). Ratio of maximum diameter of eye to width of head without eyes less than 0.26 11
Ratio of maximum diameter of eye to width of head without eyes more than 0.26 12

11(10). Fontanelle nearly triangular, length 0.2-0.3mm; wings hyaline, length of forewing 36-36.5mm; head dark brown, contrasting with much paler pronotum; anterior corners of pronotum moderately angular; southeastern Brazil (Figs. 255-257) .....*S. praecellens*
Fontanelle rounded, length 0.34-0.4; wings dark, length of forewing 27.5-28mm; head and pronotum light chestnut; anterior corners of pronotum distinctly angular; western Amazonia (Figs. 107-109) .....*S. chaquimayensis*

12(10). Length of ocellus 0.29-0.39; fontanelle usually elongate, roughly triangular; head chestnut-brown contrasting with paler pronotum; Central and southeastern Brazil (Figs. 312-314) .....*S. wheeleri*[5]
Length of ocellus 0.37-0.45; fontanelle rounded or elongate; head dark-brown; pronotum about the same color as head 13

13(12). Fontanelle rounded, length less than 0.48mm; antenna with 20 articles; Central and southeastern Brazil to Guianas (Figs. 147-149) .....*S. grandis* or *S. magnoculus*[6]
Fontanelle elongate, length more than 0.5mm; antenna with 21 articles; northern Argentina, Paraguay, southern Bolivia, and southwestern Brazil (Figs. 225-227) .....*S. obtusus*

KEY TO THE SOLDIERS OF *SYNTERMES*

Note: The terminology and measurements used in the key below are described in the Methods section. Several species are still poorly known and may show more morphological variation and wider geographical distribution than indicated in this key. The soldiers of some species show high morphological variation and may be very difficult to separate from those of other similar species because of overlap in size and morphology. Accurate identification depends on careful comparison of morphology, geographical distribution, habitat, and sometimes the nest. It is also im-

[3] Dorsal view assumes a prognathous orientation of the head.

[4] See geographical distribution. *S. cearensis* restricted to a relatively small area in northeastern Brazil.

[5] The imago of *S. peruanus*, not included in this key, is very similar, but is known only from a few, poorly preserved and incompletely sclerotized specimens from southern Peru and Northern Bolivia. See also remarks under *S. bolivianus*.

[6] *S. magnoculus* known from a few localities in Central Brazil.

portant to keep in mind that young colonies produce, at least in some species, smaller soldiers with a somewhat different morphology. This key is based exclusively on normal soldiers (i.e., from mature colonies).

1. First marginal tooth (M1, Fig. 23) of right mandible very small or absent; angle between right M1 and apical cutting edge more than 100°; left M1 small, not projecting much beyond apical cutting edge; a notch anterior to left M1 always present (Figs. 77, 170, 197, 235, 284) 2
Right M1 well-developed; angle between right M1 and apical cutting edge less than 100°; left M1 variable, but always near the middle of the mandible (Figs. 85, 141, 157, 254, 265) 10

2(1). Left M1 very close to left M2; right M1 vestigial, very close to base of mandible, or absent (Figs. 197, 284) 3
Distance from left M1 to left M2 more than 0.2 X the distance from A to M2; right M1 small but distinct (Figs. 170, 219) 6

3(2). Frontal tube very short, pore visible from dorsal view;[7] lateral margins of thoracic nota not upturned, roughly angular but not sharp (Figs. 193-197, 204-208) 4
Frontal tube prominent, pore not visible from dorsal view; lateral margins of thoracic nota upturned, very sharp and forming spines (Figs. 231-235, 280-284) 5

4(3). Sides of head converging towards front; mandibles strongly hooked at tips; postmentum widening posteriorly, with only two hairs on anterior corners; maximum width of head more than 2.9mm; Amazonia to Brazilian Atlantic forest (Figs. 193-197) .....*S. molestus*
Sides of head parallel and slightly convex; mandibles moderately hooked at tip; postmentum with posterior lateral margins parallel, two hairs on anterior corners and several hairs on posterior part; maximum width of head less than 2.9 mm; cerrado vegetation of central, southeastern and northeastern Brazil (Figs. 204-208) .*S. nanus* sp.n.

5(3). Head elongate with parallel sides; width of head less than 4mm; antenna with 19 articles; spines of meso- and metanotum short and slightly upturned; Guyana, eastern Venezuela and northern Roraima (Figs. 231-235) .....*S. parallelus*
Head short with sides converging towards front; width of head more than 5mm; antenna with 20-21 articles; spines of meso- and metanotum large and strongly upturned; western Amazonia (Figs. 280-284) .....*S. tanygnathus* sp.n.

6(2). Head elongate with parallel sides; width of head less than 0.85 X length of head; frontal tube prominent, pore not visible from dorsal view (Figs. 166, 291) 7
Head short with sides converging towards front or nearly parallel; width of head more than 0.85 X length of head; frontal tube variable 8

7(6). Maximum width of head more than 4.4mm; base of mandibles and clypeal region with many hairs (Figs. 291-295) .....*S. territus*
Maximum width of head less than 4.4mm; base of mandibles with scattered hairs; clypeal region with fewer than 10 hairs (Figs. 166-170) ....*S. longiceps*

8(6). Width of head less than 5.1mm; antenna with 19-20 articles 9
Width of head more than 5.1mm; antenna with 20-21 articles (Figs. 215-224); northern Argentina, southern Bolivia, Paraguay, and southwestern Brazil .....*S. obtusus*

9(8). Sides of head converging towards front; length of left M1 more than 0.2mm; postmentum without a protuberance near anterior margin; southern Peru and northern Bolivia (Figs. 242-246) .....*S. peruanus*
Sides of head parallel; left M1 very small, length less than 0.2 mm; postmentum with a small protuberance near anterior margin; southern Bolivia and northwestern Argentina (Figs. 73-77) .....*S. bolivianus*

10(1). Maximum width of head less than 4.3 mm 11
Maximum width of head more than 4.3 mm ..12

11(10). Antennae with 20-21 articles; length of hind tibia more than 0.8 X length of head; M1 oriented anteriorly on both mandibles; central and southeastern Brazil (Figs. 153-162) .....*S. insidians*
Antennae with 19 articles; length of hind tibia less than 0.8 X length of head; M1 oriented perpendicularly on both mandibles; Brazilian Amazonia (Figs. 171-175) .....*S. longiceps* sp.n.

12(10). Mandibles short and robust, with inflated bases (Figs. 85, 254); length of left mandible 0.38-0.45 X length of head; notal spines short and only slightly upturned 13
Mandibles moderately elongate (Figs. 141, 265); length of left mandible 0.45-0.58 X length of head; notal spines variable, but spines on meso- and metanotum conspicuously upturned 16

13(12). Head (at least anteriorly), thoracic nota and base of mandibles densely covered with hairs (Figs. 65, 250) 14
Head, thoracic nota and base of mandibles with few hairs (Figs. 81, 113) 15

14(13). Head with long, fine, curly hairs, more numerous anteriorly and on bases of mandibles; posterior margin of head distinctly three-lobed and irregular; cerrado vegetation of central Brazil (Figs. 65-69) .....*S. barbatus* sp.n.
Head with short and straight hairs, evenly distributed; posterior margin of head evenly

[7] Dorsal view assumes a prognathous orientation of the head, with top of head oriented horizontally.

rounded; central to southeastern Brazil (Figs. 250-254) ..... *S. praecellens*

15(13). Labrum short with lateral corners forming a right angle and median lobe very short; postmentum very elongate, with two hairs on anterior corners and a few or none on posterior part; right M1 small, forming an angle of more than 90° with the apical cutting edge (Figs. 81-85) ... *S. brevimalatus*
Labrum large and fleshy, with rounded corners; postmentum shorter, with numerous hairs; right M1 larger, forming an angle of about 90° with the apical cutting edge (Figs. 113-117) . *S. crassilabrum*

16(12). Head densely covered either with long, fine, curly hairs or short, straight hairs of uniform size; pronotal spines long and conical; frontal tube prominent (Figs. 54-58, 102-106, 121-125, 261-265) 17
Head capsule with scattered hairs of variable size; pronotal spines and frontal tube variable (Figs. 97-101, 302-306) 20

17(16). Head densely covered with long, fine, curly hairs (Figs. 54, 121) 18
Head densely covered with short, straight hairs (Figs. 102, 261) 19

18(17). Mandibles strongly curved; apical cutting edge of both mandibles evenly curved; M1 very large on both mandibles; central and northern Amazonia (Figs. 54-58) ..... *S. aculeosus*
Mandibles moderately curved; apical cutting edge sigmoid on both mandibles; M1 small on both mandibles; Brazilian Atlantic forest and gallery forests along Tocantins and Araguaia rivers up to Marajó Island (Figs. 121-125) ..... *S. dirus*

19(17). Width of head 5.5-6.3mm, usually less than 6.1mm; mandibles short and robust; western Amazonia (Figs. 102-106) ..... *S. chaquimayensis*
Width of head 5.7-7.6mm, usually more than 6.0mm; mandibles variable, but part anterior to M1 tends to be more elongate and slender; from Venezuela and Guianas to Mato Grosso (Figs. 261-265) ..... *S. spinosus*

20(16). Pronotal spines well developed, distinctly conical (Fig. 123); frontal tube prominent with pore oriented anteriorly, sometimes in a small depression (Figs. 90, 122); forest species 21
Pronotum with angular sides, without conical spines or with short conical spines (Figs. 139, 184); frontal tube short with pore clearly visible from dorsal view (Fig. 138); cerrado or savanna species 24

21(20). Scattered long, fine, curly hairs present on top of head (Fig. 126); sides of head nearly parallel; Brazilian Atlantic forests, from Ceará to Rio de Janeiro 22
Long, fine, curly hairs never present on head capsule; sides of head converging towards front or nearly parallel; Guianas, Amazonia, Mato Grosso 23

22(21). Width of head more than 5.2mm; frontal tube prominent; length of hind tibia 5.1-6.3mm; Brazilian Atlantic forest from Bahia to Rio de Janeiro (Figs. 126-130) ..... *S. dirus*
Width of head less than 5.2mm; frontal tube small; length of hind tibia 4.6-5.1mm forests of Ceará and western Rio Grande do Norte (Figs. 97-101) ..... *S. cearensis* sp.n.

23(21). Width of head more than 5.5mm; postmentum not inflated, only partially visible in profile; underside of head with many short, straight hairs of fairly uniform size; top of head posterior to frontal tube with many short, straight hairs; western Amazonia to Mato Grosso do Sul (Figs. 266-270) ..... *S. spinosus*[8]
Width of head less than 5.5mm; postmentum inflated, clearly visible in profile; underside of head with a few hairs of variable size; top of head posterior to frontal tube with very few or no hairs; Guianas and northeastern Brazilian Amazonia (Figs. 89-93) ..... *S. calvus*

24(20). Apical cutting edge of left mandible evenly curved, not forming a notch anterior to M1; left M1 0.97-1.24mm; width of head more than 6mm; antenna with 21 articles (Figs. 182-186) ..... *S. magnoculus*
Apical cutting edge sigmoid; width of head 5-6.6mm; left M1 0.76-1.14mm; antenna with 19-20 articles 25

25(24). Top of head posterior to frontal tube with many hairs; sides of head nearly parallel from dorsal view; M1 rather small and forming a right angle with the apical cutting edge on both mandibles; length of left mandible 2.8-3.0mm; length of hind tibia 4.7-5.3 mm (Figs. 302-306) ..... *S. wheeleri*
Top of head posterior to frontal tube with few or no hairs; sides of head converging towards front or nearly parallel; M1 larger and forming an angle of less than 90° with the apical cutting edge on both mandibles; length of left mandible 3.0-3.4mm; length of hind tibia 5.3-6.9mm (Figs. 137-146) ..... *S. grandis*[9]

TAXONOMY

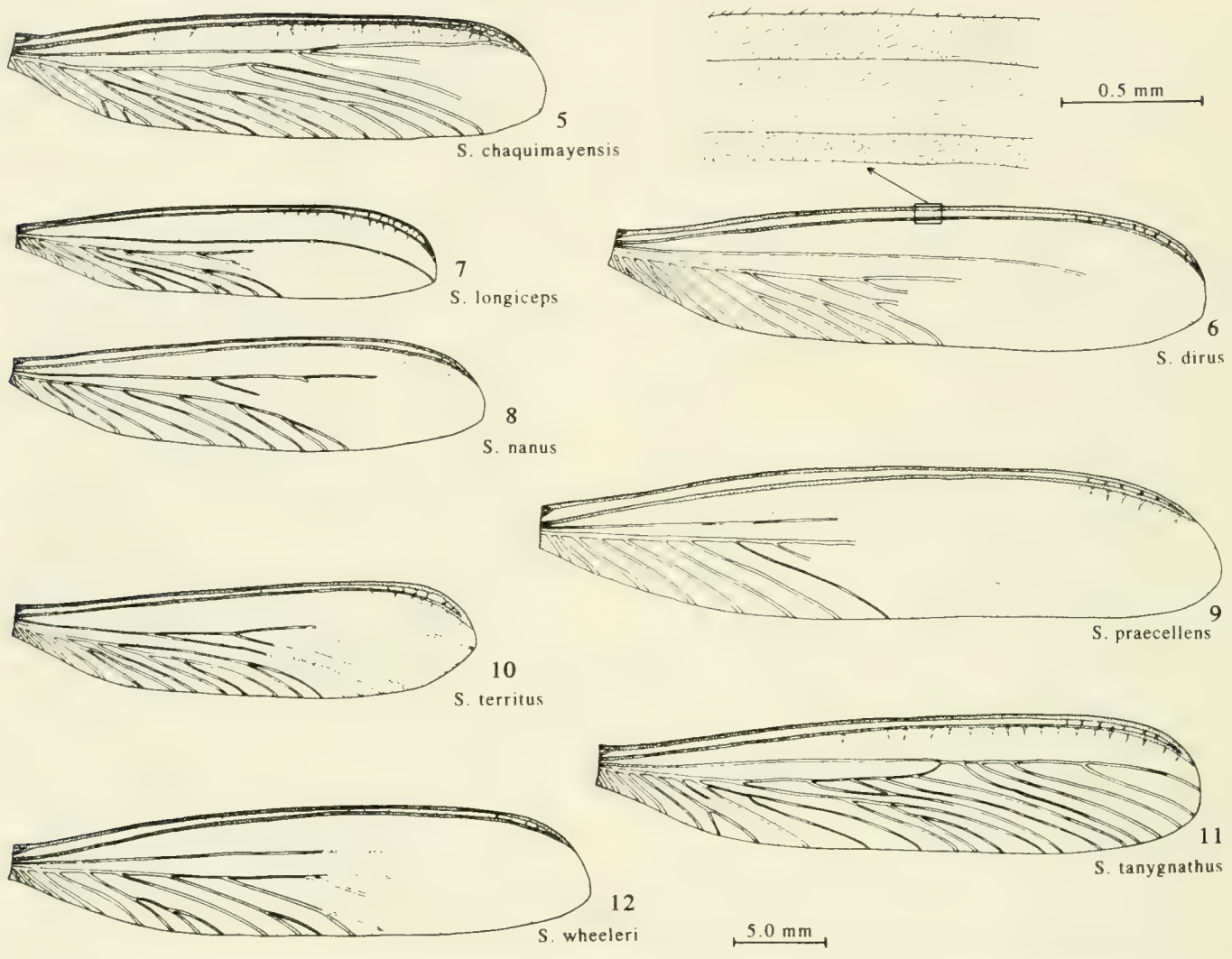
Genus *Syntermes* Holmgren

Type species: *Syntermes dirus* (Burmeister), by original designation.

Termes, Burmeister 1839: 758 [part].
Termes (*Termes*), Hagen 1858: 107; Desneux 1904: 35 [part].
Syntermes Holmgren 1910: 286 [type species designated; no description]; Holmgren 1911: 545 [taxonomic notes and key to species]; Holmgren

[8] In typical soldiers of *S. spinosus*, the top of head is densely covered with short, straight hairs. However, in some specimens from western Amazonia and Mato Grosso, fewer hairs are present on head.

[9] Soldiers of *S. grandis* show a lot of morphological variation and may be difficult to separate from those of *S. wheeleri*. Information on nest and geographical distribution will help identification.

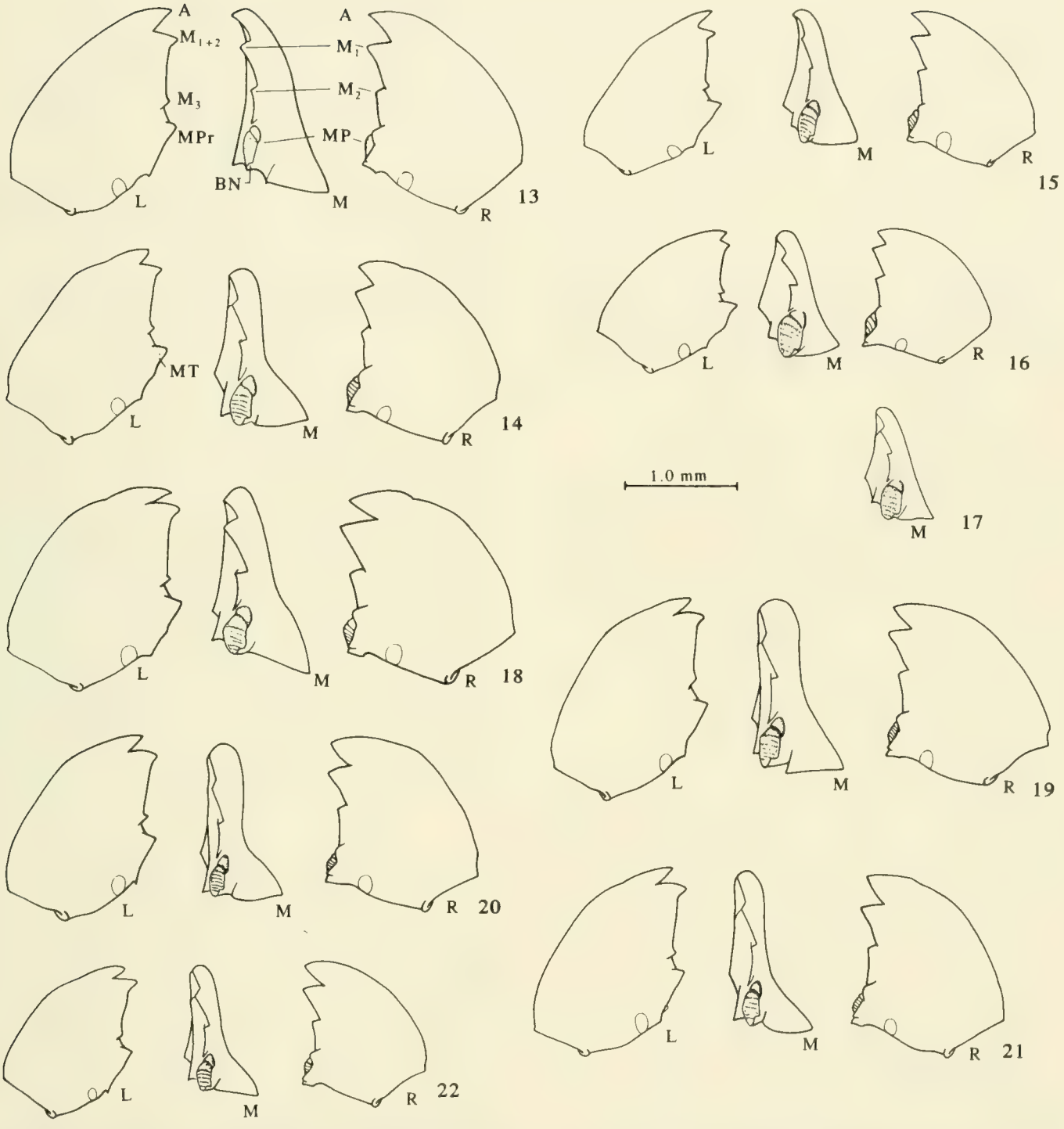


Figs. 5-12. Forewing of various *Syntermes*: 5. *S. chaquimayensis*; 6. *S. dirus*; 7. *S. longiceps*, sp.n.; 8. *S. nanus*, sp.n.; 9. *S. praecellens*; 10. *S. territus*; 11. *S. tanygnathus*, sp.n.; 12. *S. wheeleri*.

1912: 46 [description; phylogenetic relations]; Emerson 1945: 439 [revision]; Mathews 1977: 141 [diagnosis].

Imago. Head rounded, light chestnut to dark brown; pilosity variable, from a few very short hairs to numerous long ones. Relative size of eyes and ocelli variable. Fontanelle conspicuous, usually large and circular, flat or slightly convex; small and concave in a few species and slightly elongate in others. Antenna with 19 to 21 articles. Left mandible (Fig. 13) with apical tooth (A) nearly equal to first marginal tooth (M1); second marginal tooth (M2) absent; third marginal tooth (M3) short but conspicuous; cutting edge between M1 and M3 long and straight. Right mandible with A about equal to M1, sometimes a little longer; M2 smaller than A or M1; molar plate concave, small, and very narrow, with about 7 transverse ridges (less conspicuous than in workers); basal notch distinct, forming approximately a right angle. Postclypeus weakly inflated; median line visible; length less than half width. Pronotum in most species about same width as head with eyes, but sometimes wider or narrower; anterior margin raised in middle; lateral projection flat, sharply pointed or rounded; hind margin always emarginate. Tibial spur formula 3:2:2. Wings (Figs. 5-12) dark or hyaline, with two unbranched sclerotized veins distad of basal suture, one on costal border (SC + R), the other parallel to it (Rs), and weakly sclerotized and variably branched M and Cu, with distal part sometimes barely visible. Very short R1 joining SC + R distad of the basal suture. Surface of wings covered with numerous very short hairs and fine microsculpturing.

Soldier. Head large, usually short and broad, sometimes elongate; sides straight, parallel or converging towards front; head color yellow-brown; pilosity of head variable, from a few scattered hairs to dense short or long hairs. Frontal tube very short. Labrum conspicuously three-pointed, with white area on median lobe (labral gland of unknown function, probably defensive). Antennae with 19 to 21 articles. Mandibles large and robust, of variable shape and dentition; left mandible with a marginal tooth (M1) usually near middle, sometimes close to the base; second marginal tooth (M2) small and near the base; right mandible also with two marginal teeth, usually less developed than in left mandible and sometimes vestigial or absent. Pronotum with large raised anterior lobe.



Figs. 13-22. Mandibles. *Syntermes dirus*. 13. imago; 14. 4th instar male worker; 15. 3rd instar male worker; 16. 4th instar female worker; 17. 3rd instar female worker. Large worker: 18. *Syntermes grandis*; 19. *S. spinosus*; 20. *S. brevimalatus*; 21. *Syntermes longiceps*, sp.n.; 22. *S. nanus*, sp.n. L= left mandible, dorsal view; M= right mandible, mesal face; R= right mandible, dorsal view; A= apical tooth; BN= basal notch; M_1, M_2, M_3= marginal teeth; MP= molar plate; MPr= molar prominence; MT= molar tooth.

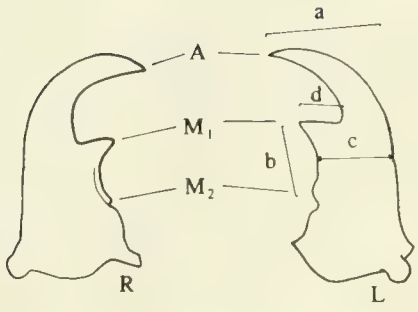
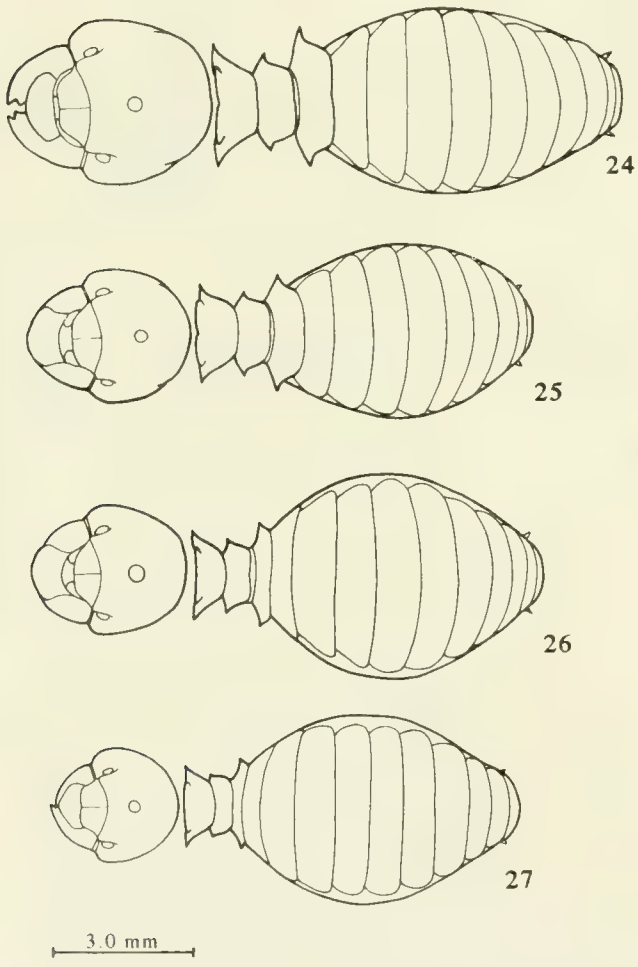


Fig. 23. Soldier mandibles, ventral view: R= right mandible; L= left mandible; A= apical tooth; M_1= first marginal tooth; M_2= second marginal tooth. Measurements: a= curvature; b= distance from tip of M_1 to tip of M_2; c= width of mandible; d= length of M_1.



Figs. 24-27. *Syntermes dirus*, workers: 24. 4th instar male ("large worker"); 25. 3rd instar male; 26. 4th instar female; 27. 3rd instar female. Hairs not shown.

Lateral edges of thoracic nota angular, usually developed into upturned sharp points or conical spines (only *S. molestus* and *S. nanus* lack spines, but sides are distinctly angular). Proximal external face of forecoxa, mesepimeron, and metepimeron with elliptic, lighter colored area with numerous pores and differentiated tissue under cuticle (exocrine glands of unknown function). Legs usually long; foretibia with numerous spine-like short bristles on inner margin, a little thicker than other leg bristles. Tibial spur formula 3:2:2.

Workers. Four forms can be recognized (Figs. 24-27): males of 3rd and 4th instars and females of 3rd and 4th instars. Male workers larger and more sclerotized, with proportionally longer mandibles with smaller molar plates (Figs. 14-17), more slender abdomens, and slightly larger notal spines (when present). Female workers pale, not differing much between instars. Male worker of 4th instar dramatically larger than that of the 3rd instar and well sclerotized, with yellow-brown head. Head of 3rd instar male yellow with irregular longitudinal stripes of paler color. Detailed descriptions will be provided only for the 4th instar male worker because it is the form most easily collected and, for many species, it is the only one available for study.

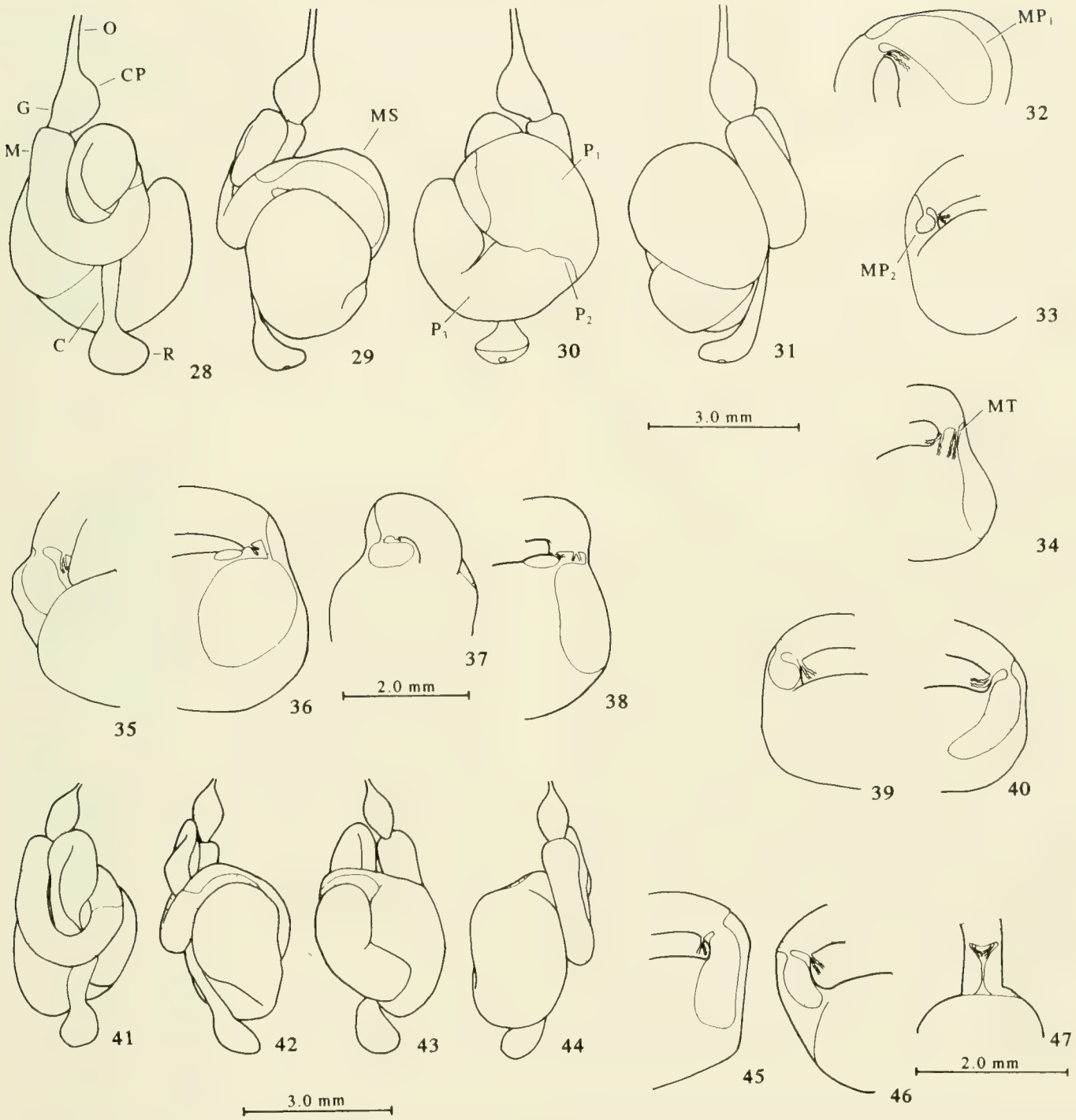
Large worker. Head nearly rounded to moderately elongate; yellow-brown; pilosity variable from few to numerous straight hairs. Fontanelle conspicuous; paler than head capsule; rounded or slightly elongate. Mandibles similar to those of imago but with much larger and wider molar region and more conspicuous molar ridges (Fig. 14). Antenna with 19 to 21 articles. Thoracic nota with angular sides or spines similar to those of soldier of same species, but smaller. Exocrine glands same as on thorax and forecoxa of soldier. Pilosity of thorax and abdomen usually similar to that of soldier. Tibiae with two rows of spine-like short bristles on inner face, more conspicuous than in soldiers. Tibial spur formula 3:2:2.

Digestive tube. Crop small and not separate from the gizzard; both forming an oval pouch of diameter similar to that of midgut; gizzard armature well-developed, its length about 1/10 that of abdomen; stomodeal valve short. Midgut relatively short. Midgut-hindgut junction with two unequal extensions of midgut tissue into hindgut, forming a mixed segment (Figs. 32-34). Malpighian tubules inserted in two pairs at midgut-hindgut junction (Fig. 34). First segment of hindgut very large, much broader than midgut. Enteric valve very wide, lacking any sclerotized armature, but with reinforced circular musculature. Paunch also well-developed, about same volume as first segment of hindgut.

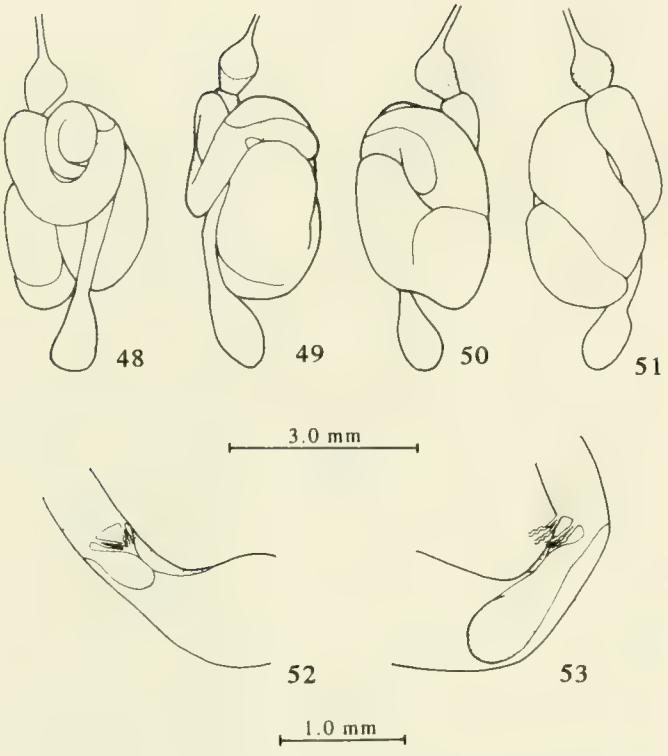
Syntermes aculeosus Emerson

Syntermes aculeosus Emerson 1945: 443 [soldier, worker]. Holotype soldier: Guyana, Oronoque River, coll. N.A. Weber, 22.vii.1936, AMNH. Paratypes: one major worker, same data as holotype.

Material examined. BRAZIL. *Amazonas*. Manaus, coll. H. Schubart, 16.iv.66, soldiers, workers [MZSP-1133]; coll. W. Paarman, 31.vii.92, alates [INPA], coll. C. Martius, 27.vii.93, one soldier, one worker [INPA]. Porto Urucu, Rio Urucu, coll. T.C.S. Pires, 19.xi.89, one soldier [MPEG-3302]. *Pará*. Faro, Rio Nhamundá, coll. T.C.S. Pires, 15.xii.88, one soldier, [MPEG-3437]; Rio Trombetas, coll. M. Lohmann, vii.94, one soldier, workers [INPA]. *Rondônia*. Presidente Médici, coll. R.B. Neto, 24.viii.84, soldiers, workers, [MPEG-2231]. U.H. Samuel, coll. A.B. Machado, 22.xi.84, soldiers, workers [MPEG-2243]. COLOMBIA. *Amazonas*, coll. S.H. Jones, soldiers [BMNH]. Bakura, coll. S.H. Jones, soldiers, alates [BMNH]. Vaupés. Querarimiri, Rio Cuduyari, coll. D. Dufour, vii.76, soldiers, [USNM]. SURINAME. Anapaike. Marowijne, coll. B. Malkin, 12.xi.63, one soldier, workers [MZSP-177]. VENEZUELA. Haut Orenoque: Maraca, coll. J. Lizot, 20.xii.69, soldiers [MNHN]. *Amazonas*. Movaca, coll. F.F.Y., 15.iv.65, soldiers [MZSP-9600]. Puerto Ayacucho, coll. C. Seiderman, i.1993, soldiers, [AMNH]. San Carlos de Rio Negro, coll. M. Blum, v.78, soldiers [MZSP-7592].



Figs. 28-47. Digestive tube: *Syntermes wheeleri*. 28. dorsal; 29. right; 30. ventral; 31. left; 32-33. mixed segment; 34. insertion of Malpighian tubules. *S. tanygnathus*, sp.n. 35. mixed segment. *S. barbatus*, sp.n. 36-37. mixed segment; 38. insertion of Malpighian tubules. *S. dirus*. 39-40. mixed segment. *Syntermes longiceps*, sp.n.. 41. dorsal; 42. right; 43. ventral; 44. left; 45-46. mixed segment; 47. insertion of Malpighian tubules. C= colon; CP= crop; G= gizzard; M= midgut; MP_1, MP_2= mesenteric prolongations on mixed segment; MS= mixed segment; MT= Malpighian tubules; O= oesophagus; P_1= first proctodeal segment; P_2= enteric valve; P_3= third proctodeal segment (paunch); R= rectum.



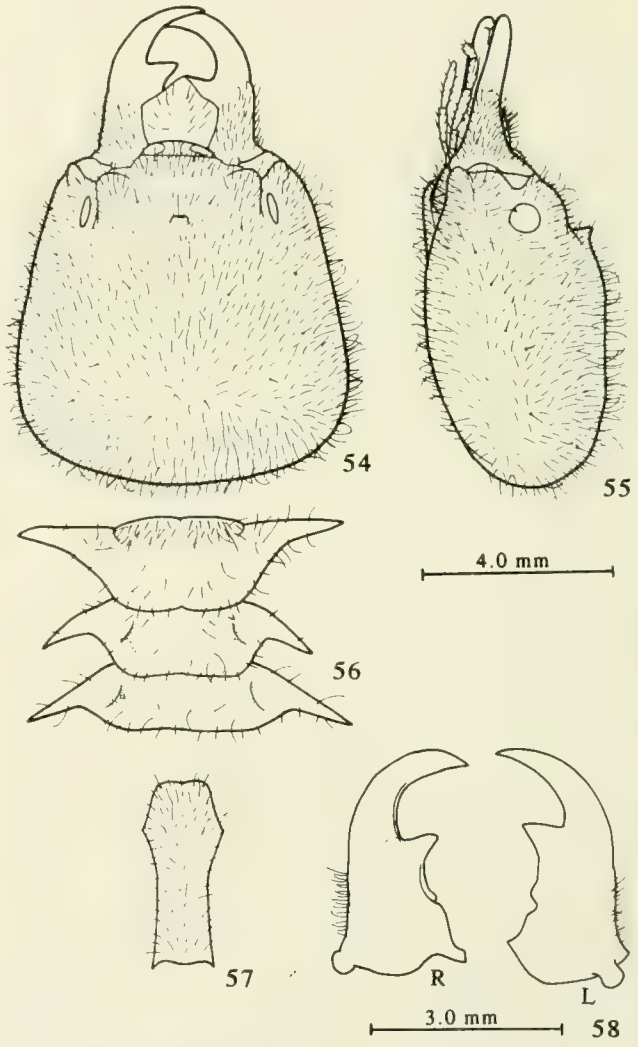
Figs. 48-53. Digestive tube: *Syntermes molestus*. 48. dorsal; 49. right; 50. ventral; 51. left; 52-53. mixed segment.

Imago (Figs. 59-61). Eyes small, diameter less than 1/4 width of head; ocelli small, length about 1/10 width of head; fontanelle large and rounded. Antenna with 20 articles. Anterior corners of pronotum sharply angular; lateral margins rounded and converging posteriorly. Wings relatively short; distal part of media and cubitus conspicuous. Head capsule with a few scattered very short hairs; postclypeus with 6-8 short hairs; pronotum with many hairs on outer margin and only a few scattered ones on surface; tergites with line of hairs on posterior margin. Head and pronotum light chestnut; tergites dark brown; wings brown to dark brown.

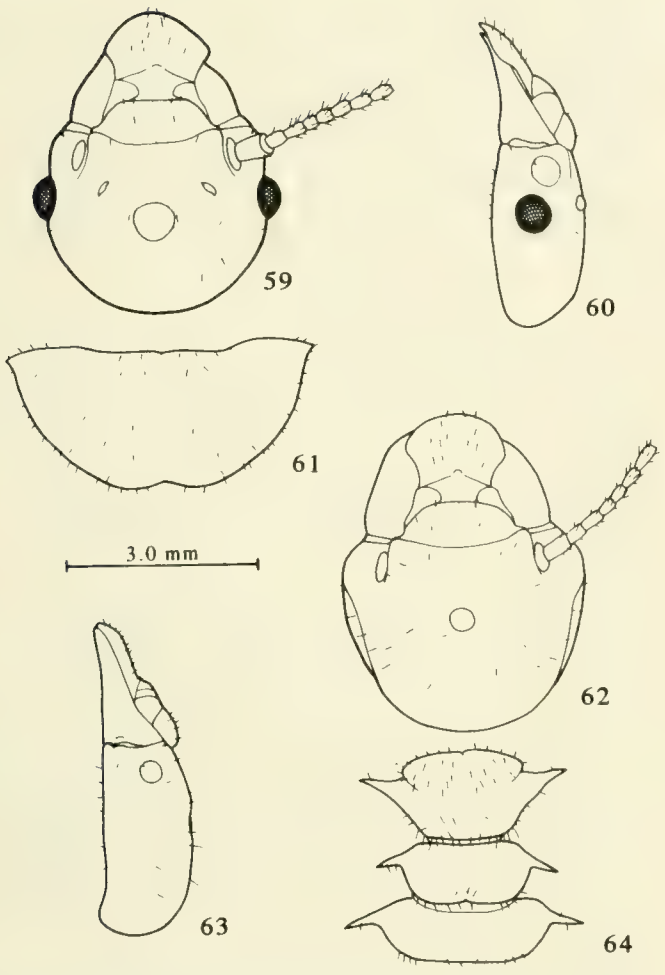
Measurements (in mm) of 3 imagoes from one colony: length of head 2.70-2.95; width of head without eyes 3.10-3.50; length of fontanelle 0.47-0.57; length of pronotum 2.00-2.30; width of pronotum 4.25-4.85; length of hind tibia 6.90-7.10; maximum diameter of eye 0.69-0.72; length of ocellus 0.27-0.35; length of forewing 26.50-30.50; width of forewing 5.70. Ratios: diameter of eye to width of head 0.21-0.23; length of ocellus to width of head 0.09-0.10; length of fontanelle to width of head 0.15-0.18; width of pronotum to width of head 1.37-1.52; length of wing to width of head 8.55-8.71; length of hind tibia to width of head 2.03-2.27.

Soldier (Figs. 54-58). Head capsule short and wide; sides straight, converging towards front; posterior margin evenly rounded. Frontal tube prominent. Lateral angle of labrum obtuse. Antenna with 20 articles. Sides of posterior part of postmentum nearly parallel. Anterior margin of pronotum emarginate (visible in posterior view only; figures show dorsal view); posterior margin slightly emarginate. Thoracic spines very long and conical. Mandibles moderately elongate and robust, strongly curved; M1 on both mandibles very large near the middle, oriented anteriorly. Apical cutting edge on both mandibles evenly curved. Head capsule with a few scattered bristles and densely covered with long, fine and curly hairs. Labrum with many bristles. Base of mandible densely covered with fine, curly hairs, shorter than those on head capsule. Postmentum with one bristle on each anterior corner and numerous fine, long and curly hairs. Pronotum with numerous bristles on anterior lobe; a few bristles on posterior margin, and scattered fine, long and curly hairs. Mesonotum and metanotum with a few bristles on posterior margin and scattered fine, long hairs. Tergites with scattered bristles on surface and posterior margins and a few long, fine hairs.

Measurements (in mm) of 11 soldiers from 11 colonies: length of head 6.30-7.10; maximum width of head 6.50-7.20; height of head excluding postmentum 3.70-4.30; length of frontal tube 0.27-0.42; length of left mandible 3.20-4.00; curvature of left mandible 1.40-2.00; distance from M1 to M2 on left mandible 0.76-1.09; width of left mandible 1.06-1.24; length of left M1 0.40-0.66; minimum width of postmentum 1.00-1.10; width of pronotum 5.40-7.10; width of metanotum 5.55-7.10; length of hind tibia 6.50-7.60. Ratio length of head to maximum width of head 0.97-1.01; length of left mandible to length of head 0.46-0.57; length of hind tibia to length of head 1.01-1.15; width of pronotum to maximum width



Figs. 54-58. *Syntermes aculeosus*, soldier. 54. head, dorsal view; 55. head, lateral view; 56. thorax, dorsal view; 57. postmentum; 58. mandibles, ventral view.



Figs. 59-64. *Syntermes aculeosus.* Imago: 59. head, dorsal view; 60. head, lateral view; 61. pronotum. Large worker: 62. head, dorsal view; 63. head, lateral view; 64. thorax.

of head 0.79-1.02; distance M1-M2 to length of left mandible 0.23-0.33; height of head to maximum width of head 0.56-0.60; width to length of left mandible 0.29-0.39.

Large worker (Figs. 62-64). Head capsule covered with sparse bristles; postclypeus with about 6 bristles. Fontanelle rounded and large. Antenna with 20 articles. Thoracic spines conical and well-developed. Mandibles similar to those of *S. dirus* (Fig. 14), except that basal notch forms a right angle. Gut superficially similar to that of *S. dirus* (Figs. 39-40) (material available was poorly preserved).

Measurements (in mm) of 5 large workers from 5 colonies: length of head 2.60-3.10; maximum width of head 3.40-3.95; length of fontanelle 0.29-0.34; width of pronotum 2.85-3.45; width of metanotum 3.00-3.75; length of hind tibia 5.20-6.00.

Comparisons. Alates similar to *S. dirus*, but with a proportionally wider and shorter pronotum and larger fontanelle. Soldiers easily distinguished based on their large size, the presence of dense long, fine and curly hairs on the head, very large thoracic spines, and large teeth on the mandibles. Some of the largest specimens of *S. dirus* may be similar in size and pilosity, but they are always measurably smaller and their mandibles have smaller teeth and a distinctly sigmoid left apical cutting edge.

Distribution and Geographical Variation. Central-northwestern portion of the Amazonian region (Fig. 318). Soldiers show considerable variation in size of the thoracic spines and of the mandibular dentition, but no geographic pattern could be recognized from the material available.

Biology. It is certainly a forest species, and one sample had the note "earth pile" which indicates its nest might be similar to that of *S. dirus.*

Syntermes barbatus, new species

Syntermes brevimalatus, Coles 1980: 51, misidentification [biology] and Baker et al. 1981 [chemical composition of the frontal gland secretion].

Holotype soldier: BRAZIL. *Distrito Federal.* Brasília: Fazenda Água Limpa, coll. H.R. Coles, 30.iv.77 [MPEG-1255]. Paratypes: two vials, same data as holotype, one with 15 soldiers [MPEG-1291] and the other with 7 soldiers and one worker [MPEG-1255].

Imago. Unknown.

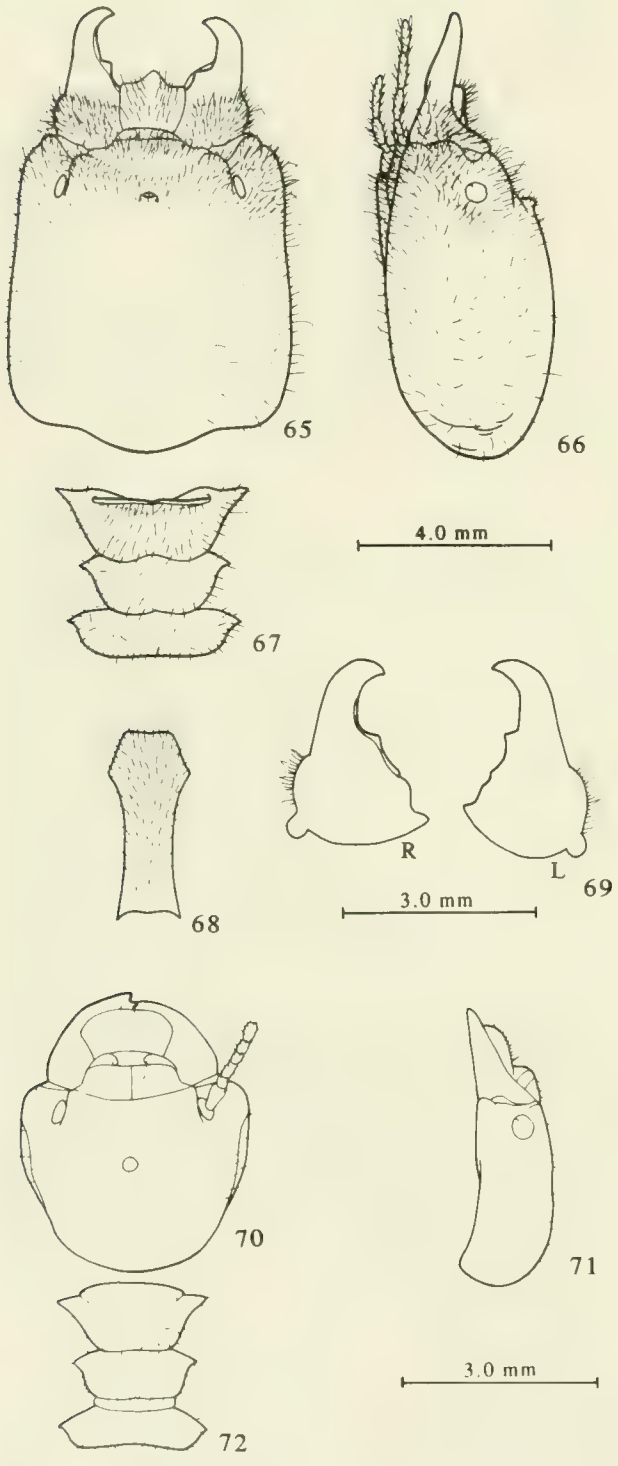
Soldier (Figs. 65-69). Head capsule short with parallel sides; length of head without mandibles about equal to its width; posterior margin of head conspicuously three-lobed and irregularly and coarsely rugose; frontal tube prominent, pore not visible from dorsal view. Labrum short, length about equal to width; lateral corners about right angular; median lobe short. Antenna with 19 or 20 articles. Postmentum not constricted in the middle, sides of posterior part nearly parallel. Mandibles very short and robust, with hooked tips; bases strongly inflated; first marginal tooth of both mandibles well-developed, near middle; angle between teeth and apical cutting edge obtuse; apical cutting edge of both mandibles evenly curved. Anterior margin of pronotum nearly rounded; posterior margin of pronotum conspicuously emarginate; thoracic spines weakly developed and oriented horizontally. Head capsule, base of mandibles and postmentum densely covered with long, fine, curly hairs, less dense on top and posterior part of head. Pronotum, mesonotum and metanotum with numerous hairs; tergites with many straight bristles plus variable number of long, fine hairs. Abdomen darker and more sclerotized than in most species.

Measurements (in mm) of 4 soldiers from 2 samples: length of head 6.40-6.60; maximum width of head 5.80-6.20; height of head excluding postmentum 3.40-3.60; length of frontal tube 0.27-0.29; length of left mandible 2.50-2.80; curvature of left mandible 0.85-0.90; distance from M1 to M2 on left mandible 0.59-0.60; width of left mandible 0.87-0.96; length of left M1 0.17-0.25; minimum width of postmentum 0.86-0.94; width of pronotum 3.60-4.00; width of metanotum 3.60-4.00; length of hind tibia 5.30-5.60. Ratios: length of head to maximum width of head 1.06-1.12; length of left mandible to length of head 0.39-0.42; length of hind tibia to length of head 0.82-0.85; width of pronotum to maximum width of head 0.61-0.67; distance M1-M2 to length of left mandible 0.21-0.24; height of head to maximum width of head 0.56-0.60; width to length of left mandible 0.31-0.38.

Large worker (Figs. 70-72). Head sparsely covered with straight bristles. Fontanelle rounded and small. Antenna with 20 articles. Thoracic spines very short. Mandibles in poor condition in only worker available. Worker gut not examined; soldier gut similar to that of *S. wheeleri*, but mixed segment is distinct (Figs. 36-38); major prolongation broadly rounded and strongly constricted at junction with midgut; minor prolongation elongate, inflated, oriented transversely, also strongly constricted at junction with midgut.

Measurements (in mm) of one large worker: length of head 2.85; maximum width of head 3.40; length of fontanelle 0.17; width of pronotum 2.25; width of metanotum 2.25; length of hind tibia 4.75.

Comparisons. The soldier of this species is very distinct, easily



Figs. 65-69. *Syntermes barbatus*, sp.n., soldier. 65. head, dorsal view; 66. head, lateral view; 67. thorax, dorsal view; 68. postmentum; 69. mandibles, ventral view.

Figs. 70-72. *Syntermes barbatus*, large worker: 70. head, dorsal view; 71. head, lateral view; 72. thorax.

distinguished by its short mandibles, dense pilosity, rugose anterior part of head, and short thoracic spines. The gut is similar only to that of *S. praecellens*.

Distribution and Geographical Variation. Known only from the type-locality (Fig. 324).

Biology. According to Coles (1980), this species lives in completely subterranean nests, in the cerrado. Foraging behavior is similar to that of other *Syntermes* species.

Syntermes bolivianus Holmgren

Syntermes bolivianus Holmgren 1911: 547-548 [soldier in key]. Lectotype soldier, here designated: Southern BOLIVIA, no data, in poor condition [AMNH]. Paralectotypes: one soldier, workers, same data as lectotype, also in poor condition [AMNH]. No types found in Holmgren's collection in NHRS.

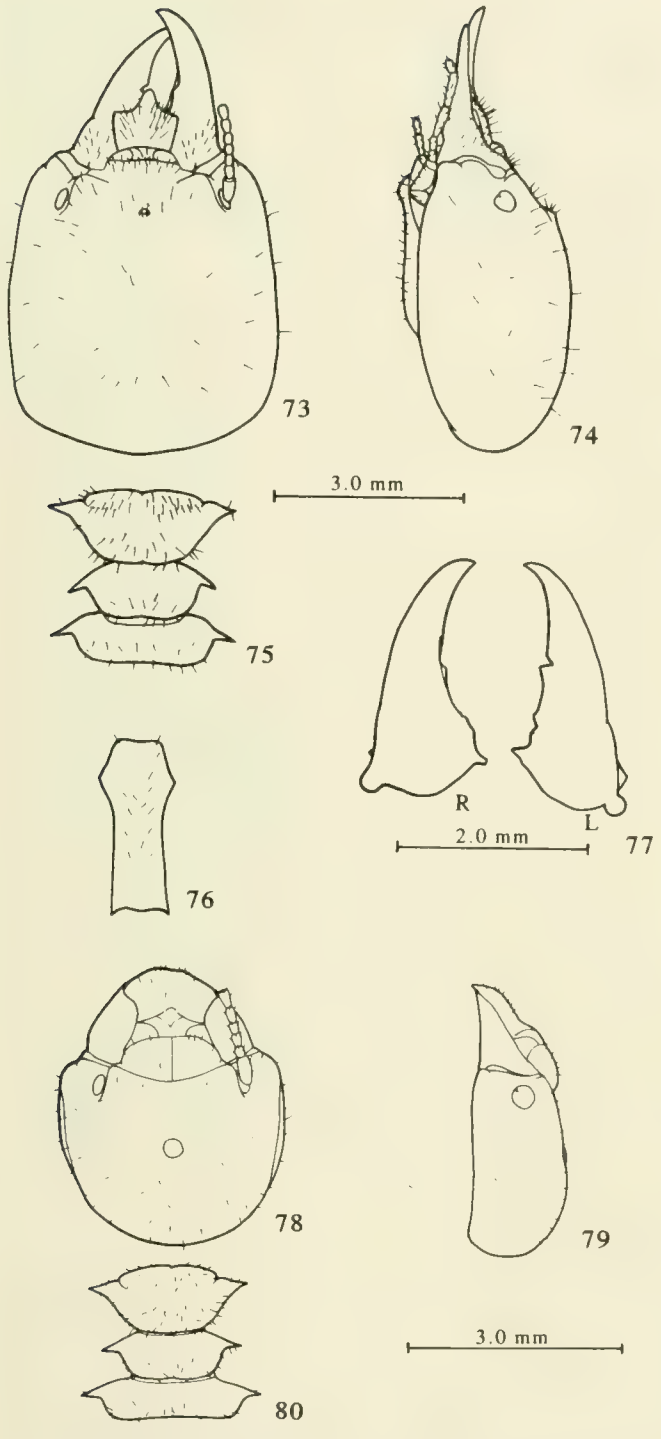
Material examined. ARGENTINA. *Santiago del Estero*. Santiago del Estero, coll. E.R. Wagner, 1911, one pinned soldier [MNHN]. *Tucumán*. Canete, 01.ix.65, one soldier, workers [MZSP-8165].

Imago. Unknown.

Soldier (Fig. 73-77). Head capsule short, length and width of head about equal, sides nearly parallel and slightly convex; posterior margin of head nearly rounded; frontal tube very short, pore clearly visible from dorsal view; labrum short, length about equal to width; lateral corners of labrum approximately a right angle; median lobe of labrum short. Antenna with 19 articles. Postmentum not constricted, sides of posterior part nearly parallel. Mandibles curved and moderately elongate; tip slightly hooked; first marginal tooth of left mandible near the middle, small, not extending much beyond the apical cutting edge; first marginal tooth of right mandible small but conspicuous, angle between anterior margin and apical cutting edge obtuse; apical cutting edge of left mandible conspicuously sigmoid, forming a notch anterior to M1; apical cutting edge of right mandible evenly curved. Anterior margin of pronotum slightly emarginate; posterior margin nearly straight; thoracic spines well-developed and upturned; pronotum with distinct but short conical spines. Head capsule from dorsal view with about 30 straight bristles; clypeal region and base of mandible with many short hairs; postmentum with two straight bristles on anterior corners plus many scattered ones. Pronotum with many bristles on entire surface, more numerous on anterior lobe; meso- and metanotum with numerous bristles on posterior half and occasionally a few on spines and lateral margins; tergites with many bristles near hind margins.

Measurements (in mm) of 3 soldiers from 3 colonies: length of head 4.35-4.80; maximum width of head 4.20-4.45; height of head excluding postmentum 2.45-2.65; length of frontal tube 0.15-0.17; length of left mandible 2.50-2.60; curvature of left mandible 0.65-0.70; distance from M1 to M2 on left mandible 0.54-0.55; width of left mandible 0.67-0.67; length of left M1 0.13-0.15; minimum width of postmentum 0.76-0.81; width of pronotum 2.95-3.10; width of metanotum 2.95-3.05; length of hind tibia 4.45-4.45. Ratio length of head to maximum width of head 1.04-1.08; length of left mandible to length of head 0.54-0.57; length of hind tibia to length of head 1.02-1.02; width of pronotum to maximum width of head 0.70-0.70; distance M1-M2 to length of left mandible 0.22-0.22; height of head to maximum width of head 0.58-0.60; width to length of left mandible 0.27-0.27.

Large worker (Figs. 78-80). Head covered with many straight bristles. Fontanelle rounded, moderately large, and convex. Antenna with 20 articles. Mandibles similar to those of *S. wheeleri*, with wide molar region. Gut not examined; available material in poor condition.



Figs. 73-77. *Syntermes bolivianus*, soldier. 73. head, dorsal view; 74. head, lateral view; 75. thorax, dorsal view; 76. postmentum; 77. mandibles, ventral view.

Figs. 78-80. *Syntermes bolivianus*. Large worker: 78. head, dorsal view; 79. head, lateral view; 80. thorax.

Measurements (in mm) of 2 large workers from 2 colonies: length of head 2.60-2.70; maximum width of head 3.10-3.10; length of fontanelle 0.30-0.34; width of pronotum 2.00-2.10; width of metanotum 2.43-2.43; length of hind tibia 3.75-3.80.

Comparisons. The soldier of *S. bolivianus* has no special diagnostic character, but can be distinguished on the basis of its relatively small size, very short frontal tube, marginal teeth weakly developed on both mandibles, and moderately developed thoracic spines. The most similar soldier is that of *S. peruanus*, which is larger and has a larger marginal tooth on the left mandible.

Distribution and Geographical Variation. Southern Bolivia and northern Argentina (Fig. 325).

Biology. No information available. Based on the geographical distribution, the most probable habitat is the chaco, an arid savanna.

Remarks. This species was considered by Emerson (1945) as a junior synonym of *S. peruanus*, based on the poor description by Holmgren (1911) and without examining any type material. Cotypes of *S. bolivianus* were later found by Emerson in Holmgren's collection and they are clearly distinct from the type of *S. peruanus*. Based on the limited material and information available, they seem to be distinct species and I am here resurrecting *S. bolivianus*. Future studies based on larger series and imagoes will be necessary to clarify the status of this species. Two undetermined alates from Argentina (Tucumán: Canete, MZSP-8164) probably belong to this species since soldiers of *S. bolivianus* were collected in the same locality. They are similar to the imagoes of *S. peruanus* and *S. wheeleri*, but I am not describing the imago of *S. bolivianus* based on that material because they were not collected with soldiers and they are not in good condition.

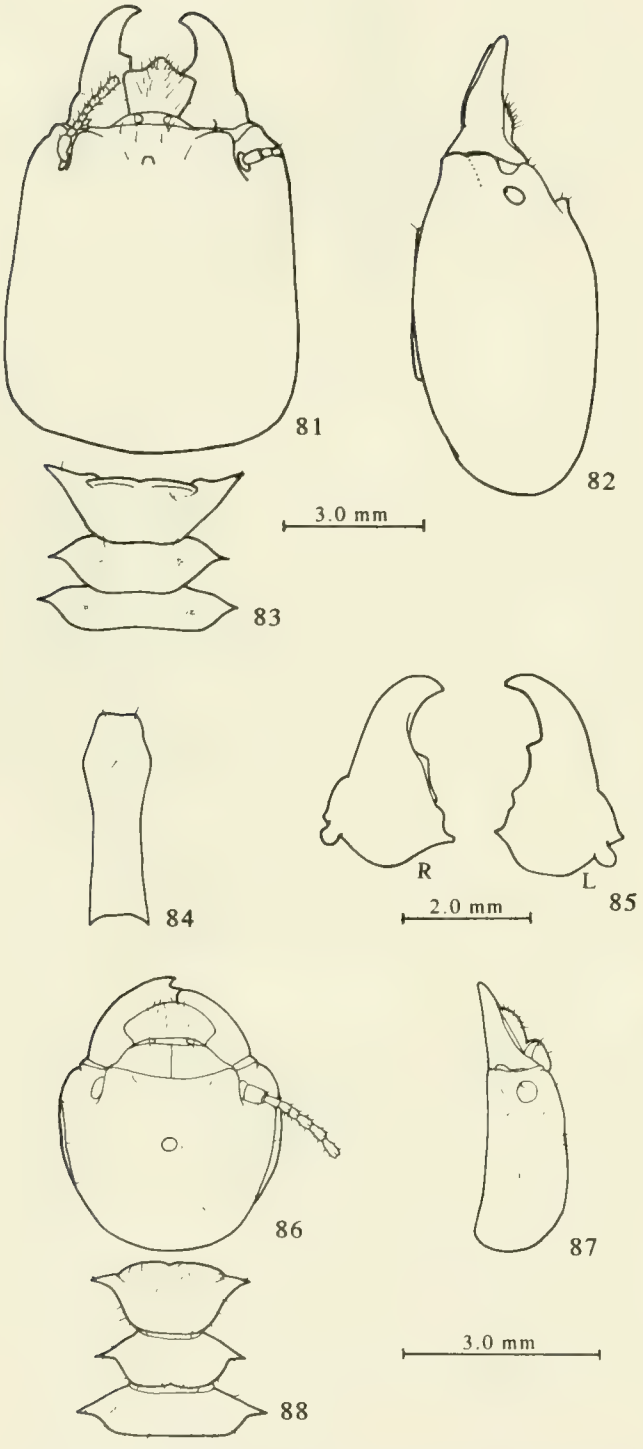
Syntermes brevimalatus Emerson

Syntermes brevimalatus Emerson 1945: 457 [soldier, worker]. Holotype soldier: GUYANA. Oronoque River, coll. N. Weber, 22.vii.36 [AMNH]. Paratypes: one soldier, workers, same data as holotype [AMNH]; one soldier, workers, same data [USNM].

Imago. Unknown.

Soldier (Figs. 81-85). Head capsule elongate with parallel sides; posterior margin of head rounded or weakly three-lobed; frontal tube prominent, pore not visible from dorsal view; labrum short, length about equal to width; lateral corner nearly forming a right angle; median lobe of labrum short. Antenna with 19 articles. Postmentum not constricted, sides of posterior part nearly parallel. Mandibles short and robust; bases strongly inflated; tips slightly hooked; both mandibles with a well-developed first marginal tooth near middle; angle between both teeth and apical cutting edge obtuse; apical cutting edge of both mandibles evenly curved. Anterior margin of pronotum conspicuously emarginate; posterior margin nearly straight; lateral projections of thoracic nota oriented horizontally; thoracic spines weakly developed; lateral corners of pronotum sharp but not forming conical spines. Head capsule in dorsal view with only about eight short bristles on clypeal region; base of mandible without hairs; postmentum with two straight bristles on anterior corners plus a few scattered ones; pronotum with only a few bristles on anterior lobe and margins; meso- and metanotum without bristles or hairs; tergites with a few bristles near hind margin.

Measurements (in mm) of 1 soldier: length of head 7.30; maximum width of head 6.30; height of head excluding postmentum 3.90; length of frontal tube 0.32; length of left mandible 2.80; curvature of left mandible 1.05; distance from M1 to M2 on left mandible 0.76; width of left mandible 0.96; length of left M1 0.24;



Figs. 81-85. *Syntermes brevimalatus*, soldier. 81. head, dorsal view; 82. head, lateral view; 83. thorax, dorsal view; 84. postmentum; 85. mandibles, ventral view.

Figs. 86-88. *Syntermes brevimalatus*. Large worker: 86. head, dorsal view; 87. head, lateral view; 88. thorax.

minimum width of postmentum 1.01; width of pronotum 4.50. Ratio length of head to maximum width of head 1.16; length of left mandible to length of head 0.38; width of pronotum to maximum width of head 0.71; distance M1-M2 to length of left mandible 0.27; height of head to maximum width of head 0.62; width to length of left mandible 0.34.

Large worker (Figs. 86-88). Head with a few scattered bristles; postclypeus with 4 bristles. Fontanelle rounded and small. Antenna with 20 articles. Thoracic spines moderately developed. Mandibles (Fig. 20) with very narrow molar plates. Gut not examined; available material in poor condition.

Measurements (in mm) of 1 large worker: length of head 2.80; maximum width of head 3.45; length of fontanelle 0.25; width of pronotum 2.50; width of metanotum 2.85; length of hind tibia 4.30.

Comparisons. The soldier of *S. brevimalatus* is very distinct and can be identified based on its elongate head with parallel sides, very short and robust mandibles, weakly developed thoracic spines and lack of hairs on most parts of the head and thorax. The most similar soldiers are those of *S. barbatus*, which is densely covered with hairs and has strongly hooked mandibles, and *S. crassilabrum*, which has longer mandibles, a large and fleshy labrum and more hairs on the head.

Distribution and Geographical Variation. Known only from the type series, a single colony from Guyana (Fig. 325).

Biology. Little information available. Field notes from the type material state: "Nesting in clay at base of tree. Openings one centimeter in diameter leading to horizontal galleries in top ten to thirty centimeters of soil." This implies that the nest is completely subterranean, since no epigeal portion is mentioned. It can also be inferred that *S. brevimalatus* lives in a forest habitat, since specimens of *S. aculeosus*, a forest species, were present in the same vial.

Syntermes calvus Emerson

Syntermes calvus Emerson 1945: 463 [soldier, worker]. Holotype soldier: GUYANA. Kartabo, coll. A.E. Emerson, 19.iv.24 [AMNH]. Paratypes: one soldier, workers, same data as holotype [AMNH].

Material examined. BRAZIL. *Pará*. Bujaru, coll. A.G. Bandeira, 22.v.79, soldiers, workers [MPEG-718]. Marituba, coll. Wygodzinsky, 10.xi.63, soldiers, workers [AMNH]. Serra dos Carajás, coll. T.P. Chaves, 22.v.84, soldiers, one worker [MPEG-2197]. Tucuruí: Chiqueirinho, coll. A.L. Nunes, 03.iv.84, soldiers [MPEG-2198]. FRENCH GUIANA. Euaclare, piste à St. Eloit, coll. C. Snyder, 3.v.91, soldiers, workers [AMNH].

Imago. Unknown.

Soldier (Figs. 89-93). Head capsule short, length and width about equal; sides converging towards front; posterior margin of head nearly rounded; frontal tube moderately prominent, pore not visible from dorsal view, usually in a small depression; labrum short, length about equal to width; lateral corners of labrum forming an obtuse angle; median lobe of labrum elongate, longer than lateral ones. Antenna with 19 or 20 articles. Postmentum strongly inflated, sides of posterior part nearly parallel or slightly concave. Mandibles curved and elongate; tip slightly hooked; first marginal tooth of left mandible near the middle and small, not extending much beyond the apical cutting edge; first marginal tooth of right mandible small; angle between apical cutting edge and M1 obtuse; apical cutting edge of left mandible conspicuously sigmoid, forming a notch anterior to M1; apical cutting edge of right mandible evenly curved. Anterior margin of pronotum slightly emarginate; posterior margin of pronotum nearly straight; lateral

projections of thoracic nota strongly upturned; thoracic spines well-developed but slender. Head capsule in dorsal view with about 30 scattered, short bristles, more numerous laterally; base of mandibles without hairs; postmentum with two straight bristles on anterior corners plus many scattered ones; pronotum with many bristles on anterior lobe and margins; meso- and metanotum with numerous bristles on posterior margin and a few on spines and side margins; tergites with many bristles near hind margin.

Measurements (in mm) of 4 soldiers from 4 colonies: length of head 5.20-5.50; maximum width of head 4.80-5.10; height of head excluding postmentum 2.80-3.00; length of frontal tube 0.08-0.25; length of left mandible 2.80-3.00; curvature of left mandible 0.95-1.15; distance from M1 to M2 on left mandible 0.62-0.69; width of left mandible 0.76-0.82; length of left M1 0.17-0.22; minimum width of postmentum 1.01-1.14; width of pronotum 3.60-3.85; width of metanotum 3.70-4.30; length of hind tibia 5.10-5.20. Ratio length of head to maximum width of head 1.04-1.15; length of left mandible to length of head 0.51-0.58; length of hind tibia to length of head 0.94-0.98; width of pronotum to maximum width of head 0.74-0.77; distance M1-M2 to length of left mandible 0.21-0.25; height of head to maximum width of head 0.56-0.59; width to length of left mandible 0.26-0.27.

Worker (Figs. 94-96). Head capsule very large relative to that of soldier (when compared to this proportion in other species of *Syntermes*); with many scattered bristles; postclypeus with about 10 bristles. Fontanelle large and rounded. Antenna with 20 articles. Thoracic spines moderately developed. Mandibles very similar to those of *S. spinosus* (Fig. 19), with well defined basal notch forming a right angle. Gut similar to that of *S. dirus* (Figs. 39-40), but minor mesenteric prolongation of mixed segment more elongate.

Measurements (in mm) of 2 large workers from 2 colonies: length of head 3.10; maximum width of head 3.50-3.55; length of fontanelle 0.30-0.42; width of pronotum 2.75-2.85; width of metanotum 2.85-2.90; length of hind tibia 4.85-4.90.

Comparisons. The soldier of *S. calvus* can be distinguished based on its elongate mandibles with relatively small teeth, conspicuously inflated postmentum, long and slender thoracic spines, and sparse head pilosity. The most similar soldiers are those of *S. peruanus*, which has a shorter frontal tube and more hairs on top of head, and *S. cearensis*, which has shorter mandibles with more conspicuous right M1 and less inflated postmentum, and usually some long, fine and curly hairs on head.

Distribution and Geographical Variation. Guianas and northeastern Brazilian Amazonia (Fig. 319). The limited material available does not allow a clear definition of geographical patterns of variation, but soldiers from Carajás and Tucuruí were a little smaller, with sides of head converging less towards front.

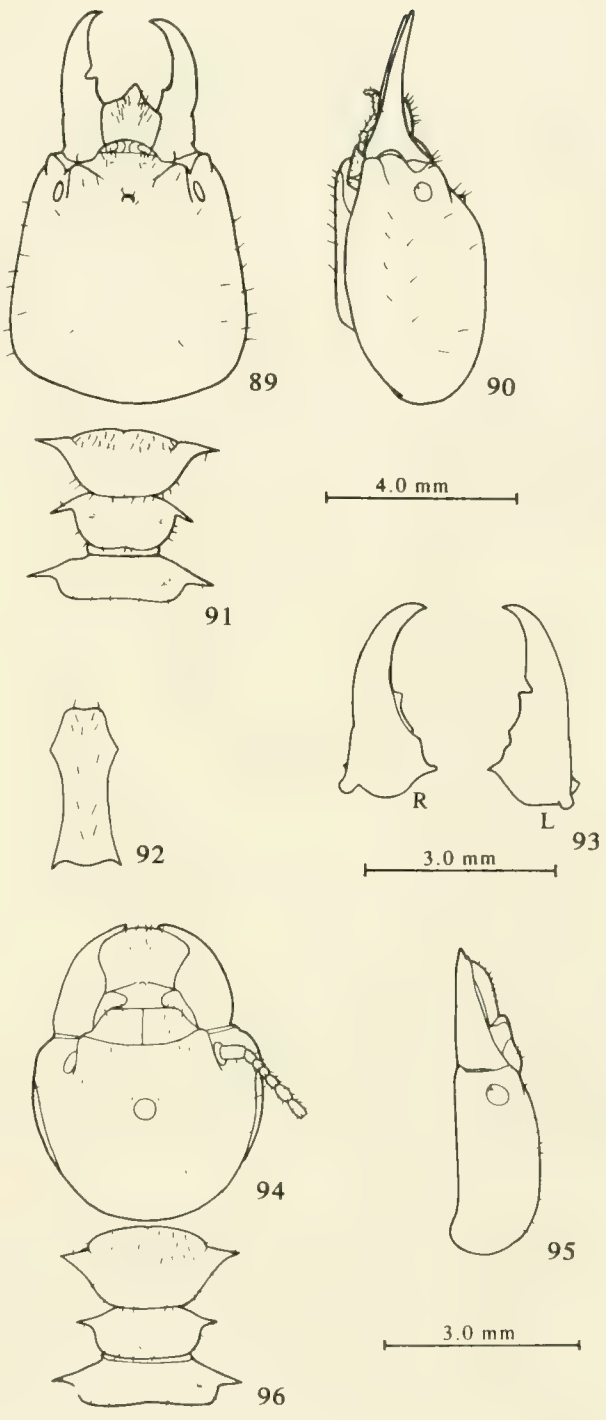
Biology. Very limited information available. Based on distribution and field notes, it seems to be a forest species. No nest information available; most probably completely subterranean.

Syntermes cearensis, new species

Holotype soldier: BRAZIL. *Ceará*. Chapada do Araripe, coll. R.L. Araujo, 21.xii.76 [MZSP-7241]. Paratypes: BRAZIL. *Ceará*. Seven soldiers, 6 alates and many workers, same data as holotype [MZSP-7241]. Crato, coll. R.L. Araujo, 10.xi.75, soldiers, workers [MZSP-6394]. Itapipoca, coll. C.R. Gonçalves, 12.xii.48, soldiers, workers [MZSP-3143]. *Rio Grande do Norte*. Martins, coll. C.R. Gonçalves, 31.v.56, soldiers [MZSP-1838].

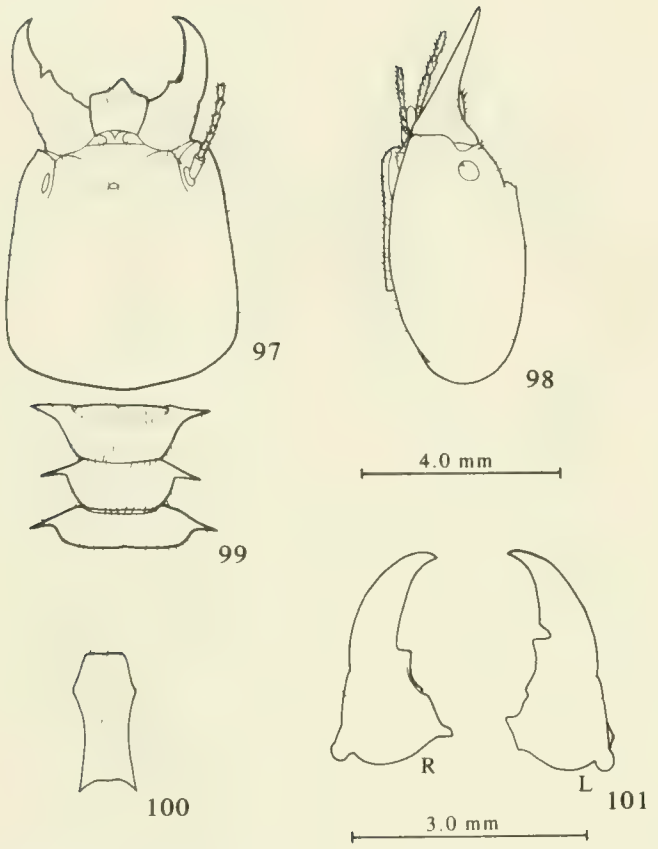
Imago. Identical to that of *S. dirus*.

Measurements (in mm) of 2 imagoes from one colony: length of head 2.60-2.65; width of head without eyes 3.05; length of



Figs. 89-93. *Syntermes calvus*, soldier. 89. head, dorsal view; 90. head, lateral view; 91. thorax, dorsal view; 92. postmentum; 93. mandibles, ventral view.

Figs. 94-96. *Syntermes calvus*. Large worker: 94. head, dorsal view; 95. head, lateral view; 96. thorax.



Figs. 97-101. *Syntermes cearensis*, sp.n., soldier. 97. head, dorsal view; 98. head, lateral view; 990. thorax, dorsal view; 100. postmentum; 101. mandibles, ventral view.

fontanelle 0.34-0.45; length of pronotum 2.00-2.15; width of pronotum 3.65-3.85; length of hind tibia 5.60; maximum diameter of eye 0.67; length of ocellus 0.25-0.27; length of forewing 30.00; width of forewing 7.70. Ratios: diameter of eye to width of head 0.22; length of ocellus to width of head 0.08-0.09; length of fontanelle to width of head 0.11-0.15; width of pronotum to width of head 1.20-1.26; length of wing to width of head 9.84; length of hind tibia to width of head 1.84.

Soldier (Fig. 97-101). Head capsule slightly elongate, sides nearly parallel; posterior margin of head nearly rounded; frontal tube prominent, pore not visible or barely visible in dorsal view; labrum short, length about equal to width; lateral corners of labrum forming an obtuse angle; median lobe short. Antenna with 20 articles. Postmentum not constricted, sides of posterior part nearly parallel. Mandibles curved and moderately elongate; tip slightly hooked; first marginal tooth of left mandible near the middle, small, not extending much beyond apical cutting edge; first marginal tooth of right mandible well developed; angle between right M1 and apical cutting edge about 90°; apical cutting edge of left mandible conspicuously sigmoid, forming a notch anterior to M1; apical cutting edge of right mandible nearly straight, except for curved distal portion. Anterior margin of pronotum slightly emarginate; posterior margin nearly straight; lateral projections of thoracic nota strongly upturned; thoracic spines well-developed, but slender. Head capsule in dorsal view with scattered long, fine hairs, some longer and curved; base of mandibles with a few to many hairs; postmentum with many fine, long hairs; pronotum with many bristles on anterior lobe and margins; meso- and metanotum with numerous bristles on posterior margin and a few on spines and side margins; tergites with many bristles near hind margin.

Measurements (in mm) of 4 soldiers from 4 colonies: length of head 4.90-5.30; maximum width of head 4.60-5.00; height of head excluding postmentum 2.60-2.90; length of frontal tube 0.18-0.25; length of left mandible 2.40-2.80; curvature of left mandible 0.90-1.15; distance from M1 to M2 on left mandible 0.59-0.69; width of left mandible 0.77-0.81; length of left M1 0.20-0.25; minimum width of postmentum 0.89-0.97; width of pronotum 3.60-4.00; width of metanotum 3.60-4.10; length of hind tibia 4.60-5.10. Ratio length of head to maximum width of head 1.04-1.10; length of left mandible to length of head 0.46-0.57; length of hind tibia to length of head 0.94-0.96; width of pronotum to maximum width of head 0.74-0.83; distance M1-M2 to length of left mandible 0.24-0.27; height of head to maximum width of head 0.56-0.58; width to length of left mandible 0.28-0.34.

Large worker. Apparently identical to that of *S. dirus*. Gut apparently also very similar to *S. dirus*, but material was too poorly preserved for detailed study.

Measurements (in mm) of 4 large workers from 2 colonies: length of head 2.55-2.85; maximum width of head 3.10-3.25; length of fontanelle 0.24-0.30; width of pronotum 2.15-2.45; width of metanotum 2.25-2.60; length of hind tibia 3.90-4.30.

Comparisons. Alates are apparently indistinguishable from those of *S. dirus*. Soldiers are conspicuously smaller than those of *S. dirus* and less hairy, and the sides of the head are more straight and parallel.

Distribution and Geographical Variation. Restricted to patches of forest in the caatinga vegetation zone in Ceará and part of Rio Grande do Norte, Brazil (Fig. 318). Little morphological variation is present in the material available.

Biology. Certainly a forest species; field notes indicate that the nest has a pile of loose soil above ground, as in *S. dirus*. One sample had workers that were parasitized by microsporid protozoans but had an otherwise normal aspect. These parasites often cause soldier-worker intercastes, as described by Silvestri (1945a) for *S. grandis*.

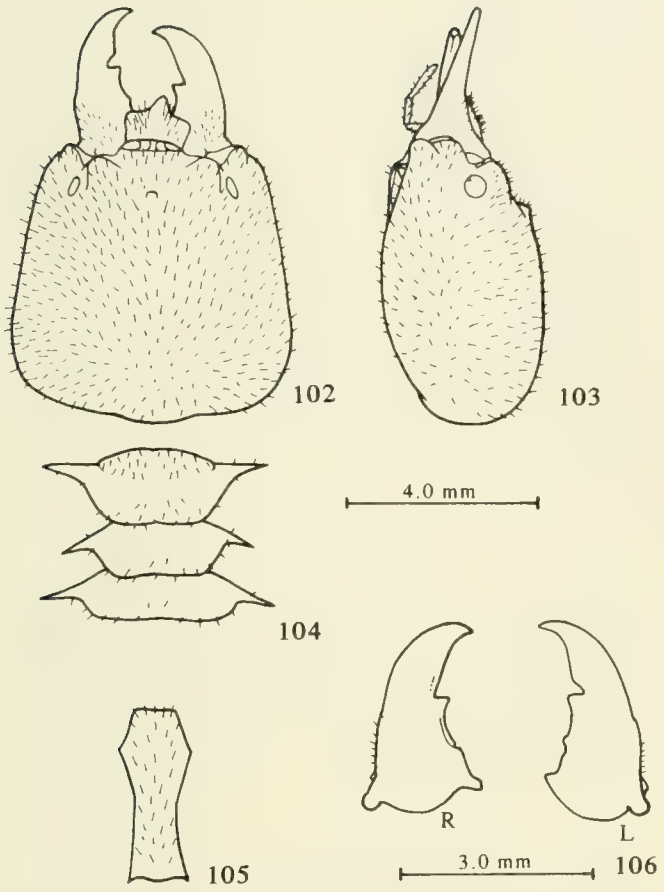
Syntermes chaquimayensis (Holmgren)

Termes chaquimayensis Holmgren 1906: 547 [soldier, worker], 662 [nest]. Lectotype soldier, here designated: PERU. Llinquipata, coll. N. Holmgren, xi 1904 [AMNH]. Paralectotypes: one soldier, same data as holotype [AMNH].

Syntermes chaquimayensis, Holmgren 1911: 548 [soldier, in key]

Syntermes chaquimayensis chaquimayensis, Emerson 1945: 447 [soldier, worker].

Material examined. BOLIVIA. No data, coll. Mulford Exploration, soldiers, workers [BMNH]. *Beni*. Huachi, coll. W.M. Mann, ix.1920, soldiers, workers [two vials in USNM and two vials in AMNH]. BRAZIL. *Acre*. Vila Taumaturgo, coll. Pe. L. Herbst, ii.62, one soldier [MZSP-147]. COLOMBIA. *Meta*. Mico, coll. J. Hendrickson, 27.xi.50, one soldier, workers [AMNH]. EQUADOR. *Napo*. Cuyabeno, coll. E. Asanza, 20.viii.81, soldiers, alates [MZSP-8868]. Limoncocha, coll. M.G. Nauman, 29.vi.71, soldiers, workers, in two vials [SEM]; coll. K. Riede, vii.1983, soldiers, workers [MNHN]. PERU. No data, one soldier, workers [ISNB]. *Cuzco*. Quillabamba, coll. W.A. Sands, 27.iv.71, soldiers, workers [BMNH]. *Huanuco*. Pampayacu, coll. R. Kaneshiro, 25.i.27, soldiers [USNM]; Tingo Maria: Rio Huallaga, coll. Vegrauil, soldiers, workers [MZSP-1815]. *Junin*. Perene, vi.1926, one soldier, workers [LEFS]; coll. J.C. Bradley, 26.vi.20, soldiers, workers in two vials [AMNH]. *Madre de Dios*. Valle Chanchamayo, 800 m, coll. Weynrauch, 1939, soldiers, workers [AMNH]. *Puno*. Chaquimayo, coll. Holmgren, soldiers, workers [ZMHU].



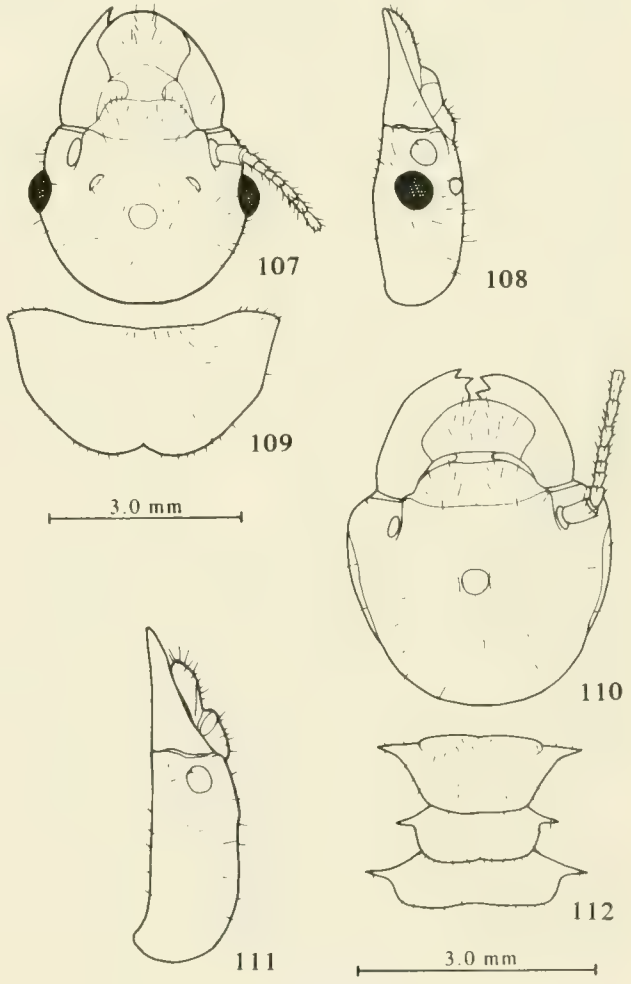
Figs. 102-106. *Syntermes chaquimayensis*, soldier. 102. head, dorsal view; 103. head, lateral view; 104. thorax, dorsal view; 105. postmentum; 106. mandibles, ventral view.

Imago (Figs. 107-109). Eyes small, less than 1/4 width of head without eyes; ocelli small; fontanelle large and rounded. Antenna with 20 articles. Anterior corners of pronotum angular, with sharp points; lateral margins of pronotum nearly straight and converging posteriorly. Wings (Fig. 5) relatively short and dark; distal part of media and cubitus conspicuous. Head capsule covered with numerous long hairs; postclypeus with about 16 hairs; pronotum with many hairs on outer margin and only a few scattered ones on surface; tergites with many hairs from middle to posterior margin. Head light chestnut; pronotum light chestnut; tergites chestnut-brown; sternites light chestnut.

Measurements (in mm) of 4 imagoes from one colony: length of head 2.60-2.75; width of head without eyes 3.05-3.25; length of fontanelle 0.34-0.40; length of pronotum 2.10-2.30; width of pronotum 4.00-4.30; length of hind tibia 6.30-6.80; maximum diameter of eye 0.67-0.72; length of ocellus 0.32-0.34; length of forewing 27.50-28.00; width of forewing 6.70-7.60. Ratios: diameter of eye to width of head 0.22-0.23; length of ocellus to width of head 0.10-0.11; length of fontanelle to width of head 0.11-0.13; width of pronotum to width of head 1.31-1.35; length of wing to width of head 8.62-9.03; length of hind tibia to width of head 2.00-2.13.

Soldier (Figs. 102-106). Head capsule short, length and width about equal, sides converging towards front; posterior margin nearly rounded or weakly three-lobed; frontal tube prominent, pore not visible in dorsal view. Labrum short, length about equal to width; lateral corners about equal to a right angle; median lobe short. Antenna with 19 to 20 articles. Postmentum not constricted, sides of posterior part nearly parallel or slightly concave; mandibles short, curved, robust; tip slightly hooked; first marginal tooth of left mandible usually small, not extending much beyond apical cutting edge, sometimes larger; first marginal tooth of right mandible well-developed; angle between right M1 and apical cutting edge acute; apical cutting edge of left mandible conspicuously sigmoid, forming a notch anterior to M1; apical cutting edge of right mandible slightly sigmoid or nearly straight. Anterior and posterior margin of pronotum slightly emarginate; lateral projections of thoracic nota strongly upturned; thoracic spines well-developed. Head capsule densely covered with short, straight bristles; base of mandibles with numerous short hairs; postmentum densely covered with short, straight bristles; pronotum with many bristles, more numerous on anterior lobe; meso- and metanotum with numerous bristles on posterior margin and a few on spines and lateral margins; tergites with numerous bristles on posterior half.

Measurements (in mm) of 5 soldiers from 5 colonies: length of head 5.60-6.20; maximum width of head 5.60-6.10; height of head excluding postmentum 3.05-3.50; length of frontal tube 0.13-0.22; length of left mandible 2.70-3.30; curvature of left mandible 1.25-



Figs. 107-112. *Syntermes chaquimayensis.* Imago: 107. head, dorsal view; 108. head, lateral view; 109. pronotum. Large worker: 110. head, dorsal view; 111. head, lateral view; 112. thorax.

1.50; distance from M1 to M2 on left mandible 0.59-0.79; width of left mandible 0.94-1.11; length of left M1 0.25-0.40; minimum width of postmentum 0.89-1.06; width of pronotum 4.20-4.80; width of metanotum 4.30-4.85; length of hind tibia 5.40-5.80. Ratio length of head to maximum width of head 0.97-1.02; length of left mandible to length of head 0.45-0.59; length of hind tibia to length of head 0.90-0.95; width of pronotum to maximum width of head 0.75-0.81; distance M1-M2 to length of left mandible 0.22-0.28; height of head to maximum width of head 0.53-0.57; width to length of left mandible 0.31-0.40.

Large worker (Figs. 110-112). Head capsule with several scattered straight bristles; postclypeus with about 12 bristles. Fontanelle large and rounded. Antenna with 19 or 20 articles. Thoracic spines well developed. Mandibles very similar to those of *S. spinosus*. Gut apparently similar to that of *S. dirus*, but material was poorly preserved.

Measurements (in mm) of 4 large workers from 4 colonies: length of head 2.60-2.85; maximum width of head 3.25-3.55; length of fontanelle 0.22-0.32; width of pronotum 2.50-2.80; width of metanotum 2.50-3.05; length of hind tibia 4.40-4.80.

Comparisons. The imago of *S. chaquimayensis* is similar to those of *S. dirus* and *S. spinosus*, but has a distinct pilosity on the head capsule. The most similar soldier is that of *S. spinosus*, which is usually larger and has longer mandibles with larger teeth. However, soldiers of *S. spinosus* show wide variation and there seems to be some size overlap.

Distribution and Geographical Variation. A narrow zone, from Colombia to Bolivia, parallel to the Andes (Fig. 320). Apparently this species is limited to a certain range of altitude, around 300 to 800 m.

Biology. *S. chaquimayensis* is a rain forest species and, according to Holmgren's (1906: 662) description, its nest is similar to that of *S. dirus*.

Syntermes crassilabrum, new species

Holotype soldier. BRAZIL. *Amazonas*. Manaus: Reserva Ducke, coll. F.B. Apolinario, 23.i.91 [INPA-895]. Paratypes: BRAZIL. *Rondônia*. Indeterminate locality, 1985, one soldier, workers [MPEG-3923].

Imago. Unknown.

Soldier (Figs. 113-117). Head capsule elongate with sides slightly converging towards front or nearly parallel; posterior margin of head nearly rounded; frontal tube prominent, pore not visible in dorsal view; labrum large and fleshy, longer than width, with rounded corners, median lobe short. Antenna with 19 to 20 articles. Postmentum not constricted, sides of posterior part nearly parallel. Mandibles short and robust; bases strongly inflated; tip slightly hooked; first marginal tooth of left mandible large, extending well beyond apical cutting edge; first marginal tooth of right mandible large; angle between right M1 and apical cutting edge about 90°; apical cutting edge of left mandible slightly sigmoid; apical cutting edge of right mandible evenly curved. Anterior and posterior margins of pronotum slightly emarginate. Lateral projections of thorax slightly upturned; thoracic spines small but conspicuous. Head capsule in dorsal view with 30-40 scattered short, straight bristles, more numerous laterally and anteriorly; clypeal region with about 12 hairs; base of mandible with a few short hairs; postmentum densely covered with short, straight bristles; pronotum with many bristles on anterior lobe and margins; meso- and metanotum with numerous bristles on posterior margin and a few on spines and lateral margins; tergites with numerous bristles on posterior half.

Measurements (in mm) of 2 soldiers from 2 colonies: length of head 6.30-6.80; maximum width of head 5.90-6.20; height of head excluding postmentum 3.30-3.80; length of frontal tube 0.25-0.29; length of left mandible 2.60-2.70; curvature of left mandible 1.05-1.10; distance from M1 to M2 on left mandible 0.72-0.72; width of left mandible 0.99-1.06; length of left M1 0.32-0.35; minimum width of postmentum 1.06-1.06; width of pronotum 4.00-4.40; width of metanotum 4.00-4.40; length of hind tibia 5.80-5.90. Ratio length of head to maximum width of head 1.07-1.10; length of left mandible to length of head 0.40-0.41; length of hind tibia to length of head 0.85-0.94; width of pronotum to maximum width of head 0.65-0.75; distance M1-M2 to length of left mandible 0.27-0.28; height of head to maximum width of head 0.56-0.61; width to length of left mandible 0.37-0.41.

Large worker (Fig. 118-120). Head capsule with scattered straight bristles. Postclypeus with about 10 bristles. Fontanelle large and rounded. Thoracic spines weakly developed. Mandibles similar to those of *S. spinosus*, with a 90° basal notch. Gut superficially similar to that of *S. dirus*, but material available was poorly preserved; mesenteric prolongations of mixed segments touch one another.

Measurements (in mm) of 2 large workers from 1 colony: length of head 2.70-2.70; maximum width of head 3.35-3.45; length of fontanelle 0.34-0.34; width of pronotum 2.35-2.35; width of metanotum 2.65-2.65; length of hind tibia 4.50-4.50.

Comparisons. The most similar soldier is that of *S. brevimalatus* which has shorter mandibles, a more elongate head, fewer hairs on head and thorax, and smaller marginal teeth on both mandibles. A distinctive character of the soldier of *S. crassilabrum* is the large and fleshy labrum.

Distribution and Geographical Variation. Known from only two localities in central and western Brazilian Amazonia (Fig. 325).

Biology. No information available. Based on the localities, it is probably a rain forest species.

Syntermes dirus (Burmeister)

Termes dirus Burmeister 1839: 766 [alate, soldier]. Lectotype alate female, here designated: BRAZIL. Rio (probably Rio de Janeiro), coll. V. Olfers. Nr. 2763 [ZMHU]. Paralectotypes: two alate females, same data as lectotype [ZMHU]; two alates and one soldier, "Brazil, Winthem" [MCZ]. The syntype soldier in ZMHU is not *S. dirus*.

Syntermes dirus, Holmgren 1911: 545 [key]; Emerson 1945: 459 [redescription, part].

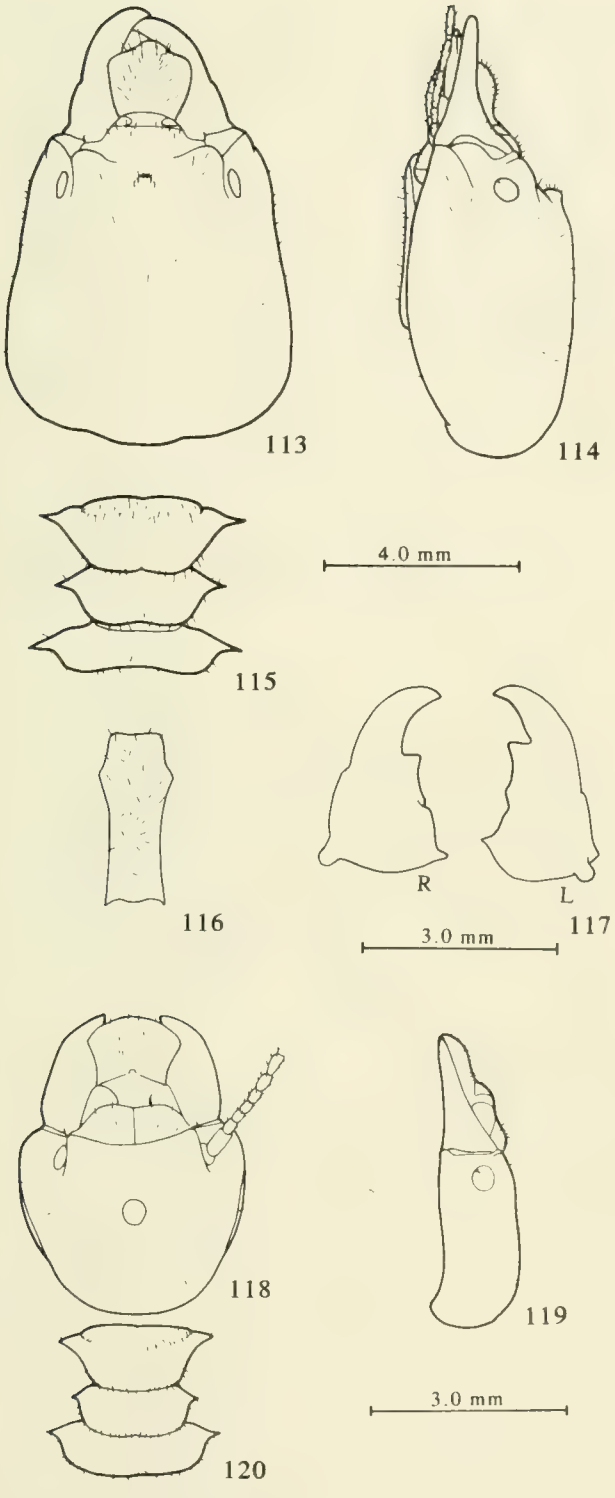
Termes obscurum Blanchard 1840: 47 [alate]. From Rio de Janeiro, Brazil. Type not located, but based on the description and the locality there is little doubt that this is *S. dirus*. Synonymized by Hagen (1858: 151).

Termes dubius Rambur 1842: 309 [soldier]. From Brazil. Type not located. Synonymized by Hagen (1858: 155).

Syntermes hageni, Snyder 1924: 28, Fig. 21, misidentification [soldier].

Syntermes sp.n., Baker et al. 1981, misidentification [chemical composition of the frontal gland secretion].

Material examined. BRAZIL. *Bahia*. Andaraí, coll. E.M. Cancello, 13.xii.90, soldiers, workers [MZSP-9743 and 9745]. Iguassu, coll. A. Roman, 31.vii.24, one soldier, workers [AMNH]. Ilhéus, coll. Jacques Labie, 22.xii.86, soldiers, workers [MZSP-8996]. Itabuna, coll. R.L. Araujo, 25.ii.72, one soldier, workers [MZSP-5010]. Itapetinga, coll. R.L. Araujo, 28.ii.72, soldiers, workers [MZSP-5009]. Olivença, coll. R.L. Araujo, 26.ii.72, soldiers, workers [MZSP-5006]. Poções, coll. R.L. Araujo, 22.xii.76, soldiers, workers [MZSP-7255]. São José, Rio Utinga, coll. A.G. Bandeira, 29.xii.94, soldiers, workers [UFPB]. Urucuca, coll. R.L. Araujo, 22.ii.72, soldiers, workers [MZSP-5008]. Vila Nova, coll. E. Gorbe, 1908, soldiers, workers [MZSP-1850]. *Distrito Federal*. Brasília: Fazenda Água Limpa, coll. D. Brandão, 1981, soldiers, one worker [UFG-153]. *Espírito Santo*. coll. H. Fruhstorfer, one alate [BMNH]; soldiers, workers [LEFS]; coll. E. Garbe, ii.1906, soldiers, workers, one alate [MZSP-1142]; coll. A.N. Ab'Saber, 15.xi.69, soldiers [MZSP-4739]. Aracruz, coll.



Figs. 113-117. *Syntermes crassilabrum*, sp.n., soldier. 113. head, dorsal view; 114. head, lateral view; 115. thorax, dorsal view; 116. postmentum; 117. mandibles, ventral view.

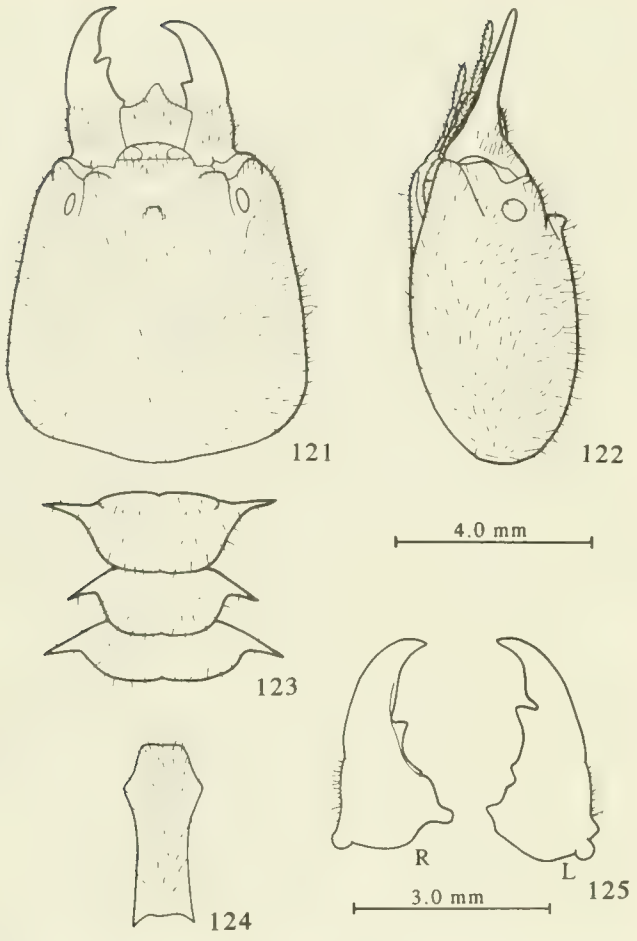
Figs. 118-120. *Syntermes crassilabrum*. Large worker: 118. head, dorsal view; 119. head, lateral view; 120. thorax.

R.L. Araujo, 27.v.54, soldiers [MZSP-4169]. Chapada de Carapina, coll. R.L. Araujo, 29.v.54, soldiers, workers [MZSP-4181]. S.J. de Petropólis, coll. R.L. Araujo, 25.v.54, soldiers, workers [MZSP-4131]. *Goiás*. Goiânia, coll. A. Barcelos, 30.iii.90, soldiers, workers [UFG-378]. Ilha do Bananal, coll. D. Brandão, 01.x.87, soldiers, workers [UFG-331]. *Maranhão*. Montes Altos, coll. A.G. Bandeira, 10.i.77, soldiers, workers [MPEG-217]. *Mato Grosso do Sul*. Costa Rica, expedição IQUSP, 12.ii.86, soldiers, workers, alates [MZSP-8769]. *Minas Gerais*. Belo Horizonte, coll. R.L. Araujo, 23.xii.51, soldiers, workers, alates [MZSP-3422]; coll. R.L. Araujo, 30.xii.53, soldiers, workers [MZSP-4034]. Coronel Fabriciano, coll. A.B. Pereira, ix.55, soldiers [MZSP-1860]. Francisco Sá, coll. R.L. Araujo, 18.xii.75, soldiers, workers [MZSP-5919 and 5929]. Machacalis, coll. F.S. Pereira, xii.54, one soldier, workers [MZSP-1839]. Montezumia, coll. R.L. Araujo, 16.xii.50, one soldier, one worker [AMNH]; coll. R.L. Araujo, 12.i.52, soldiers, workers [MZSP-3406]. Rio Preto, coll. C.R. Goncalves, 22.i.68, soldiers [MZSP-370]. Viçosa, coll. B. Nogueira, iii.72, soldiers, workers [MZSP-5349]; coll. H.R. Coles, 07.xi.76, soldiers [MZSP-9294], coll. O.F. Souza, 15.xii.93, one soldier, one worker [MEUV]. *Pará*. Marajó Isl., Anajás, coll. W.L. Overal, 09.xii.82, soldiers [MPEG-1449]. Tucuruí, Canoal, coll. A.G. Bandeira, 28.iii.84, one soldier, workers [MPEG-1990]. *Rio Grande do Sul*. Porto Alegre, coll. C.H. Reiniger, 2.i.40, one soldier [AMNH]. Rio Grande, coll. H.v. Ihering, one soldier [MCZ]. *Rio de Janeiro*. Campo Grande, coll. A.G. Araujo e Silva, 17.ii.44, soldiers, workers [MZSP-4659]. Duque de Caxias, coll. Jose Amancio, soldiers, workers [MZSP-4657]. Ilha Grande, coll. Muth & Sick, iv.43, one soldier, one worker [AMNH]. Ilha do Governador, coll. G. Pabst, ix.67, soldiers, workers [MZSP-374]; coll. M.L. Oliveira, vi.29, soldiers, workers [MZSP-2961]. Itaguaí, coll. R.L. Araujo, 15.iii.68, soldiers, workers [MZSP-1846]. Jacarepaguá, coll. F.M. Oliveira, 25.iii.68, one soldier, workers [MZSP-1814]. Rio de Janeiro, coll. Wygodzinsky, 5.xi.63, soldiers, workers [AMNH]; coll. H. Schubart, 09.viii.62, soldiers, workers [MZSP-65]; coll. R.L. Araujo, 18.ii.64, soldiers, one worker [MZSP-157]; coll. Lima & Garcia, 09.xi.70, alates [MZSP-4853]. S.J. da Barra, coll. M.M. Chaves, 06.ix.63, soldiers, workers [MZSP-1818]. Santa Cruz, coll. Costa Lima, 30.ix.36, one soldier, one worker [AMNH]. *São Paulo*. Nova Europa, coll. K. Lenko, 26.iv.68, soldiers, workers [MZSP-1827, MZSP-1828 and MZSP-1829]; coll. K. Lenko, 18.vi.65, soldiers, workers [MZSP-1832]. Rincão, i.45, alates [MZSP-2722]. São Paulo, coll. Stevens, one alate [BMNH].

Imago (Figs. 131-133). Eyes small, less than 1/4 width of head without eyes; ocelli small; fontanelle rounded and large. Antenna with 20 articles. Anterior corners of pronotum angular, with sharp points; lateral margins slightly sigmoid, with anterior half nearly parallel. Wings (Fig. 6) dark and relatively short; distal part of media and cubitus conspicuous. Head capsule with scattered very short hairs, sometimes barely visible; postclypeus with 6-8 short hairs; pronotum with many hairs on outer margin and only a few scattered ones on surface; tergites with very short hairs on posterior margin; head and pronotum light chestnut; tergites chestnut-brown; sternites light chestnut.

Measurements (in mm) of 7 imagoes from 4 colonies: length of head 2.45-2.90; width of head without eyes 3.05-3.40; length of fontanelle 0.30-0.50; length of pronotum 2.20-2.40; width of pronotum 3.90-4.45; length of hind tibia 6.00-6.60; maximum diameter of eye 0.71-0.74; length of ocellus 0.25-0.37; length of forewing 29.50-34.00; width of forewing 6.90-8.10. Ratios: diameter of eye to width of head 0.21-0.23; length of ocellus to width of head 0.08-0.11; length of fontanelle to width of head 0.10-0.15; width of pronotum to width of head 1.21-1.33; length of wing to width of head 8.94-10.33; length of hind tibia to width of head 1.88-2.10.

Soldier (Figs. 121-130). Head capsule short, length and width of head about equal; sides nearly parallel or converging slightly towards front; posterior margin of head nearly rounded or weakly three-lobed; frontal tube prominent and broad, pore not visible in dorsal view; labrum short, length about equal to width; lateral



Figs. 121-125. *Syntermes dirus*, soldier. 121. head, dorsal view; 122. head, lateral view; 123. thorax, dorsal view; 124. postmentum; 125. mandibles, ventral view.

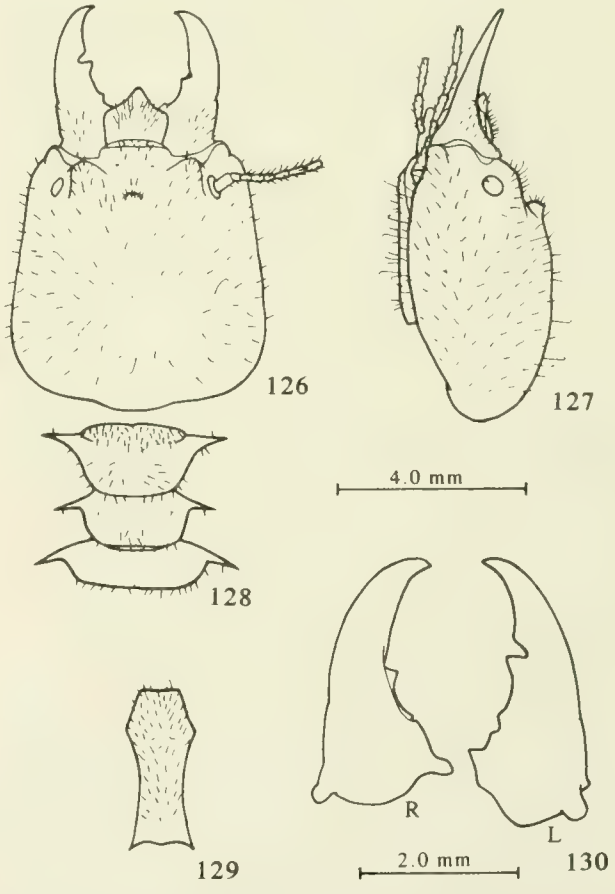
corners of labrum about equal to a right angle; median lobe of labrum short. Antenna with 20 articles. Postmentum not constricted, sides of posterior part nearly parallel. Mandibles curved and moderately elongate; tip slightly hooked; first marginal tooth of left mandible near the middle and small, not extending much beyond apical cutting edge; first marginal tooth of right mandible small but conspicuous; angle between right M1 and apical cutting edge about 90°; apical cutting edge of left mandible conspicuously sigmoid, forming a notch anterior to M1; apical cutting edge of right mandible slightly sigmoid. Anterior margin of pronotum slightly emarginate; posterior margin nearly straight; lateral projections of thorax strongly upturned; thoracic spines long and conical. Head capsule covered with variable number of long, fine, curly hairs and some straight hairs; base of mandibles with numerous short hairs; postmentum densely covered with fine, long, curly hairs; pronotum with numerous hairs; meso- and metanotum with numerous hairs near hind and lateral margins; tergites with numerous bristles on posterior half.

Measurements (in mm) of 19 soldiers from 18 colonies: length of head 5.10-7.00; maximum width of head 4.80-6.70; height of head excluding postmentum 2.70-3.80; length of frontal tube 0.24-0.37; length of left mandible 2.70-3.10; curvature of left mandible 0.85-1.50; distance from M1 to M2 on left mandible 0.62-0.94; width of left mandible 0.77-1.04; length of left M1 0.18-0.35; minimum width of postmentum 0.79-1.09; width of pronotum 3.50-5.00; width of metanotum 3.60-5.70; length of hind tibia 4.80-6.80. Ratio length of head to maximum width of head 0.98-1.10; length of left mandible to length of head 0.44-0.56; length of hind tibia to length of head 0.87-1.02; width of pronotum to maximum width of head 0.66-0.84; distance M1-M2 to length of left mandible 0.22-0.30; height of head to maximum width of head 0.54-0.60; width to length of left mandible 0.27-0.34.

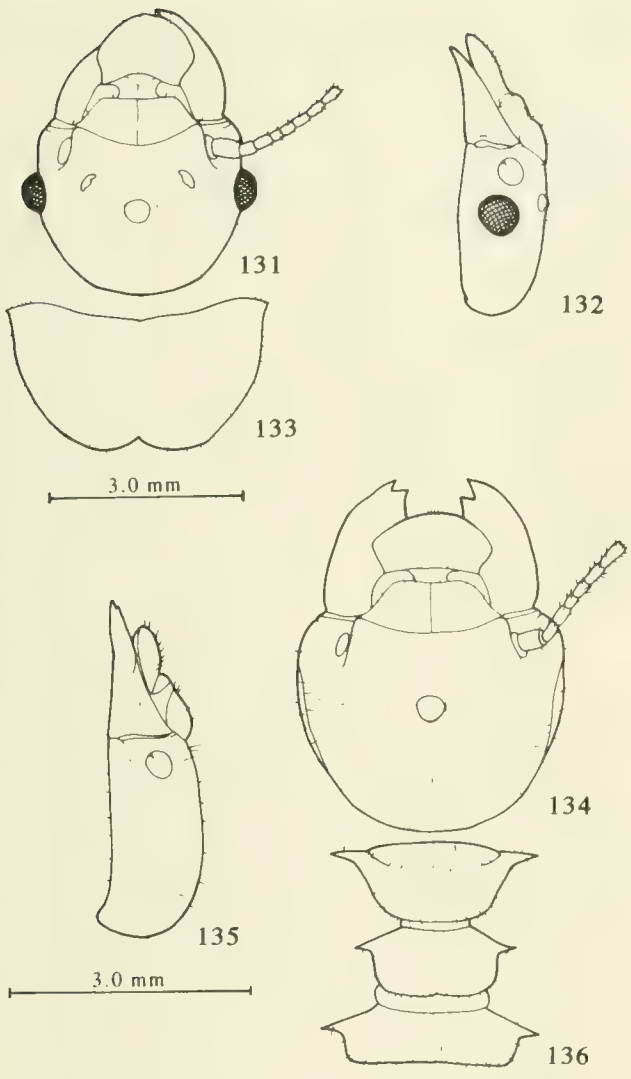
Worker (Figs. 134-136). Head capsule covered with numerous short, straight hairs. Postclypeus with about 12 hairs. Fontanelle large and rounded. Thoracic spines well developed. Antenna with 20 articles. Mandibles (Fig. 14) with relatively narrow molar plate and basal notch forming an obtuse angle. Gut described in detail by Kovoor (1969: 198). Large midgut prolongation of the mixed segment tongue-shaped and very narrow (Fig. 39); small prolongation shaped like a golf club (Fig. 40).

Measurements (in mm) of 9 large workers from 9 colonies: length of head 2.65-2.85; maximum width of head 3.20-3.40; length of fontanelle 0.24-0.34; width of pronotum 2.30-2.75; width of metanotum 2.40-2.85; length of hind tibia 4.30-4.80.

Comparisons. The imago of *S. dirus* is indistinguishable from that of *S. cearensis*, and very similar to those of *S. aculeosus*, *S. spinosus*, *S. chaquimayensis* and *S. tanygnathus*. *S. aculeosus* has wider pronotum and larger fontanelle; *S. spinosus* and *S. chaquimayensis* have longer and more numerous hairs on head; and *S. tanyg-*



Figs. 126-130. *Syntermes dirus*, soldier from a different colony. 126. head, dorsal view; 127. head, lateral view; 128. thorax, dorsal view; 129. postmentum; 130. mandibles, ventral view.



Figs. 131-136. *Syntermes dirus*. Imago: 131, head, dorsal view; 132, head, lateral view; 133, pronotum. Large worker: 134, head, dorsal view; 135, head, lateral view; 136, thorax.

nathus has antenna with 21 articles. The soldier of *S. dirus* can be distinguished by the numerous long, fine and curly hairs on head, the long and conical thoracic spines, the prominent and wide frontal tube, and the well marked notch anterior to left Md. Density of long, fine hairs is variable, however.

Distribution and Geographical Variation. *S. dirus* is common on the Brazilian Atlantic forests, from Bahia to Rio Grande do Sul, but it is also found in gallery forests in Central Brazil and along the Tocantins and Araguaia rivers, with one record from the Marajó Island (Fig. 318). Soldiers from Rio de Janeiro to Bahia tend to be a little smaller and with less numerous hairs on the head than those of other regions, but with some overlap. The number of alates available for study is rather small, and they do not show any geographical pattern of variation.

Biology. Although *S. dirus* is a common species in densely populated areas of the Brazilian Coast, the biology of this species is still very poorly known. It is certainly a forest species, but may occasionally be found in pastures. Its nest (Fig. 2) is described in detail here for the first time (see section on nests above).

Remarks. Klug was considered for some time as the author of this species, but, as already noted by Snyder (1924: 26), his was just a manuscript name and was never published. The type series was apparently a mixture of alates and soldiers collected separately, and at least two of those soldiers were not *S. dirus*, but *S. wheeleri* instead. The fact that Burmeister did describe the soldier caste seems to have been ignored by earlier authors, but it is not possible to determine whether he based his description on the *S. wheeleri* specimens, the *S. dirus* ones, or both. *Termes cephalotes* Rambur 1842: 309 was listed by Emerson (1945: 460) as a possible synonym of *S. dirus*, but since the type seems to be lost and the description is useless, that name should be considered of uncertain position. Based on Rambur's description, it is impossible to tell whether *T. cephalotes* is a *Syntermes* species, or whether it refers to soldier or imago caste.

Syntermes grandis (Rambur)

Termes grandis Rambur 1842: 306 [alate]. Holotype alate: FRENCH GUIANA, Cayenne. No data, in poor condition [ISNB]. No paratypes or syntypes known.

Syntermes grandis, Holmgren 1911: 547 [key]; Emerson 1945: 451 [imago, soldier]; Baker et al. 1981 [chemical composition of the frontal gland secretion].

Termes decumanus Erichson 1848: 582 [alate only, but lectotype soldier is *S. spinosus*]

Syntermes dirus f. *hageni* Holmgren 1911: 547 [soldier]. Holotype soldier: "T. Hageni n. sp. revid. Hagen 1856, Brazil", in poor condition [AMNH].

Syntermes hageni, Emerson 1945: 454 [soldier].

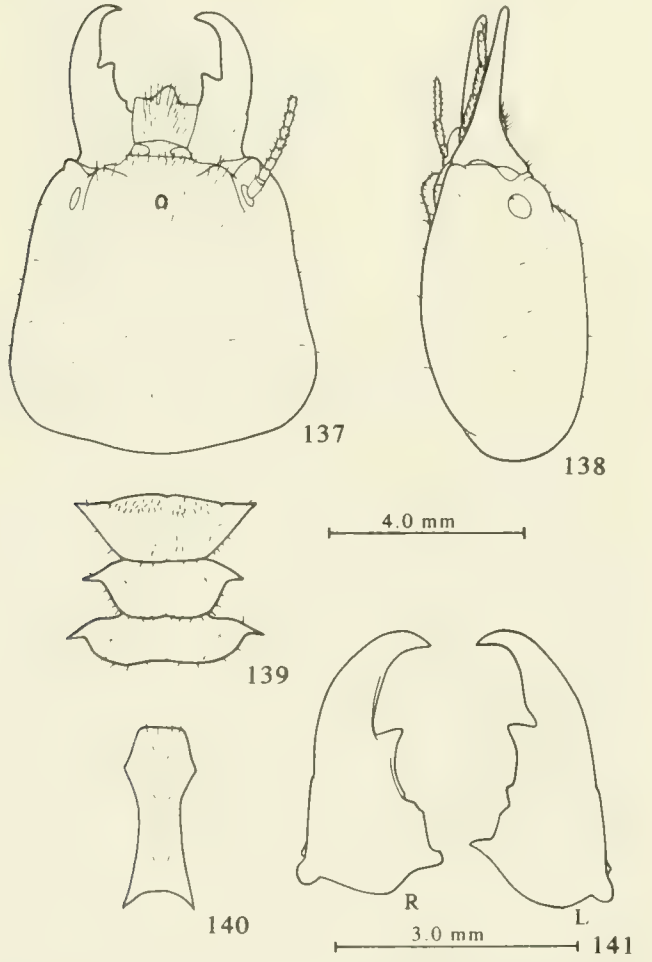
Syntermes lighti Emerson 1945: 453 [soldier]. Holotype soldier: BOLIVIA. *Beni*, Villa Bella, coll. J.D. Haseman, 9.x.1909 [AMNH].

Material examined. BOLIVIA. *Beni*, Villa Bela, coll. J.D. Haseman, 9.x.09, soldiers [AMNH]. BRAZIL. *Amapá*. Aporema, coll. R. Constantino, 26.x.89, one soldier, workers [MPEG-3234]. Curiaú, coll. R. Constantino, 18.x.89, soldiers, workers [MPEG-3168]. *Amazonas*. Humaitá, coll. R. Constantino, 18.ix.90, soldiers, workers [MPEG-3755 and MPEG-3757]; coll. R. Constantino, 20.ix.90, soldiers, workers [MPEG-3788 and MPEG-3797]. *Distrito Federal*. Brasília, coll. H.R. Coles, 26.viii.77, soldiers, workers, alates [UnB]; coll. R.L. Araujo, x.61, soldiers, workers, alates [MZSP-153]; coll. H.R. Coles, 28.iv.77, soldiers, workers [MPEG-2707]. *Goiás*. Goiânia, coll. D. Brandão, 24.iii.83, one soldier, workers [UFG-34]; coll. D. Brandão, 05.v.83, soldiers, workers [UFG-49; UFG-51]; coll. D. Brandão, xi.84, soldiers, workers [UFG-184]; coll. A.M. Curado, 28.v.86, soldiers, workers [UFG-229]. Parque Nacional das Emas, coll. K. Redford, ix.1981, soldiers, workers [MZSP-9780]. *Mato Grosso*. Caiçara, coll. Natterer, one soldier, one worker [AMNH]. Xavantina, coll. A.G.A. Mathews, 29.ix.68, soldiers [BMNH]; coll. A.G.A. Mathews, 24.x.68, large series with many soldiers, workers, alates and a queen, in several vials [BMNH]; coll. A.G.A. Mathews, xi.67, alates [BMNH]; coll. A.G.A. Mathews, one soldier, workers [BMNH]; coll. H.R. Coles, i.77, soldiers, workers [MZSP-9295]; coll. H. Sick, 30.xi.46, alates [AMNH]. *Mato Grosso do Sul*. 18°20'S 52°50'W, coll. A.E. Mill, 07.vii.80, soldiers [MZSP-8404]; coll. Mill & Redford, 09.vii.80, soldiers [MZSP-8405]. Campo Grande, coll. R.L. Araujo, 25.x.53, soldiers, workers [MZSP-3983]. Três Lagoas, coll. K. Lenko, 28.iii.65, one soldier, workers [MZSP-1010]; coll. F. Silvestri, 26.vii.35, soldiers, workers [LEFS]. *Minas Gerais*. Sete Lagoas, coll. G. Cosenza, xi.71, soldiers, workers [MZSP-8566]. Uberaba, coll. R.L. Araujo, 09.xi.72, soldiers, workers [MZSP-5696]. *Paraná*, coll. L. Zolessi, vii.54, one soldier [MZSP-1813]. *Pará*. Areia, coll. C.R. Goncalves, 29.viii.47, one soldier, one worker [MZSP-4660]. João Pessoa, coll. A. Macedo, soldiers, one worker [MZSP-4658]. Santarém, coll. Thayer Expedition, soldiers [MCZ; AMNH; USNM]; coll. H.W. Bates, soldiers, workers [BMNH]; coll. Stevens, 1854, alates [BMNH]. *Pernambuco*. Engenho Camorim, coll. B. Dantas, 06.viii.58, soldiers, workers [MZSP-4687]. Jaboatão,

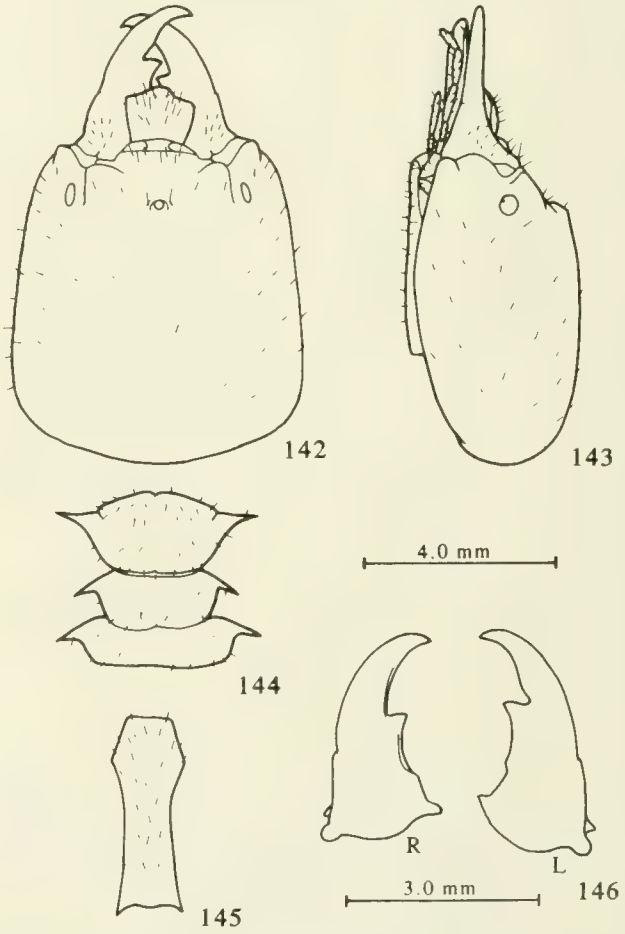
coll. J. Rangel, 02.ii.52, soldiers [MZSP-1849]. Usina Aliança, coll. C.R. Goncalves, x.67, soldiers [MZSP-1861]. *Roraima.* Coll. B. Bentley, 1974, soldiers, workers [AMNH]; coll. K. Kitvama, 19.iii.72, soldiers, workers [MZSP-5312]. Arabupu, Mt. Roraima, coll. G.H. Tate, xii.1927, soldiers, workers [AMNH]. Boa Vista, coll. C.R. Goncalves, 09.vii.53, soldiers, workers [MZSP-4662]; coll. C.R. Goncalves, 09.xi.53, soldiers, workers [MZSP-4666]. Ireng River, 1911, soldiers [AMNH]. Monte Roraima, coll. J.G. Myers, soldiers, workers [USNM]. Vista Alegre, one soldier, workers [AMNH]; coll. Bequaert, one soldier, workers [USNM]. *Sergipe.* Estância, coll. R.L. Araujo, 23.xi.75, one soldier, workers [MZSP-6449]. *São Paulo.* Agudos, coll. W.K., 31.v.52, soldiers, workers [MZSP-1840]. Itu, coll. Kloss & Silva, 05.xi.61, alates [MZSP-1865]. Ribeirão Preto, coll. R. Castro, 27.vi.83, soldiers, workers [MZSP-8268]. S.J. do Rio Preto, coll. Machado, 08.vi.66, soldiers, workers [MZSP-1831]. S.J. dos Campos, coll. F. Mariconi, 26.iv.65, soldiers, workers [MZSP-1816 and MZSP-1830]; coll. F. Mariconi, 30.vii.65, soldiers, workers [MZSP-1799]. FRENCH GUIANA. Cayenne, soldiers [ISNB]; 1905, soldiers [MNHN]. GUYANA. Lethem, coll. G.K. Rutherford, 1956, soldiers, workers [BMNH]. Pakaraima Mts., Upper Ireng R., coll. J.G. Myers, soldiers, workers [USNM]. SURINAME. Coesoewijne Savanne, coll. Geijskes, 7.ii.57, soldiers, workers [MZSP-9764]. Jodensavanne, coll. M.A. Knoppe, vi.57, soldiers, workers [MZSP-9767]. VENEZUELA. *Bolivar.* Akuriman, coll. Anduze, xi.40, soldiers, workers [AMNH]. Santa Elena de Vairen, coll. P.E. Vanzolini, 16.xii.88, one soldier, workers [MZSP-9122].

Imago (Figs. 147-149). Eyes large, diameter more than 1/4 width of head to about 1/3 width of head; ocelli relatively large; fontanelle rounded and small to medium. Antenna with 20 articles. Anterior corners of pronotum rounded to moderately angular; lateral margins of pronotum straight and nearly parallel in anterior half to rounded and converging posteriorly. Wings long; distal part of media and cubitus inconspicuous. Head capsule densely covered with straight bristles; postclypeus with about 16 bristles; pronotum with many hairs on outer margin and surface; tergites with many hairs from middle to posterior margin. Head dark brown; pronotum chestnutbrown; tergites dark brown; sternites light chestnut; wings hyaline, except for brownish proximal and costal areas.

Measurements (in mm) of 9 imagoes from 6 colonies: length of head 2.90-3.10; width of head without eyes 3.30-3.70; length of fontanelle 0.32-0.47; length of pronotum 2.15-2.40; width of pronotum 3.65-4.25; length of hind tibia 6.30-7.10; maximum diameter of eye 0.92-1.08; length of ocellus 0.37-0.44; length of forewing 29.50-32.00; width of forewing 6.90-7.70. Ratios: diameter of eye to



Figs. 137-141. *Syntermes grandis*, soldier from Suriname. 137. head, dorsal view; 138. head, lateral view; 139. thorax, dorsal view; 140. postmentum; 141. mandibles, ventral view.



Figs. 142-146. *Syntermes grandis*, soldier from Bolivia, paratype of *S. lighti.* 142. head, dorsal view; 143. head, lateral view; 144. thorax, dorsal view; 145. postmentum; 146. mandibles, ventral view.

width of head 0.27-0.33; length of ocellus to width of head 0.11-0.13; length of fontanelle to width of head 0.10-0.14; width of pronotum to width of head 1.09-1.23; length of wing to width of head 8.55-9.55; length of hind tibia to width of head 1.84-2.12.

Soldier (Figs. 137-146). Head capsule short, length and width of head about equal, sides converging slightly to strongly towards front; posterior margin of head rounded or weakly three-lobed; frontal tube very short, pore clearly visible in dorsal view; labrum short, length about equal to width; lateral corners nearly equal to a right angle; median lobe of labrum short. Antenna with 20 articles. Postmentum slightly constricted near the middle, sides of posterior part concave. Mandibles curved and moderately elongate; tip slightly to conspicuously hooked; first marginal tooth of left mandible near the middle and large, extending well beyond apical cutting edge; first marginal tooth of right mandible large; angle between right M1 and apical cutting edge less than 90°; apical cutting edge of left mandible conspicuously sigmoid; apical cutting edge of right mandible evenly curved. Anterior margin of pronotum nearly rounded to slightly emarginate; posterior margin nearly straight; thoracic spines small and strongly upturned; pronotum with or without distinct conical spines. Head capsule with many short, straight bristles, more numerous laterally; base of mandibles with many short hairs; postmentum densely covered with short, straight bristles; pronotum with many bristles, more numerous on anterior lobe; meso- and metanotum with numerous bristles on posterior margin and a few on spines and lateral margins; tergites with numerous bristles on posterior half.

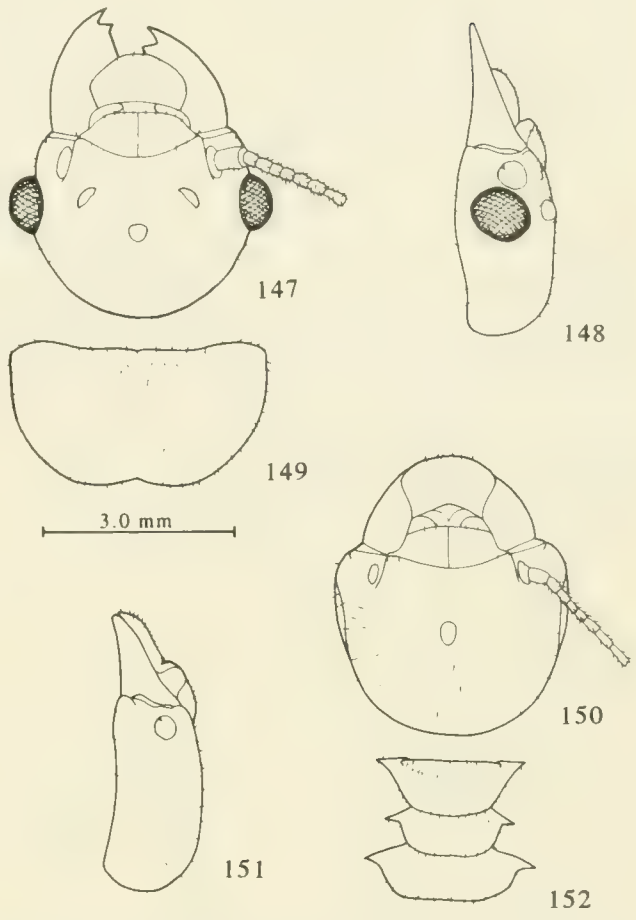
Measurements (in mm) of 28 soldiers from 28 colonies: length of head 5.60-6.80; maximum width of head 5.65-6.60; height of head excluding postmentum 3.10-3.70; length of frontal tube 0.08-0.30; length of left mandible 3.00-3.40; curvature of left mandible 1.20-1.60; distance from M1 to M2 on left mandible 0.67-0.92; width of left mandible 0.89-1.14; length of left M1 0.25-0.47; minimum width of postmentum 0.82-1.04; width of pronotum 3.45-4.30; width of metanotum 3.55-4.35; length of hind tibia 5.30-6.90. Ratio length of head to maximum width of head 0.94-1.12; length of left mandible to length of head 0.48-0.57; length of hind tibia to length of head 0.84-1.10; width of pronotum to maximum width of head 0.58-0.74; distance M1-M2 to length of left mandible 0.22-0.28; height of head to maximum width of head 0.51-0.59; width to length of left mandible 0.28-0.35.

Worker (Figs. 150-152). Head capsule with many straight bristles; postclypeus with about 10 bristles. Fontanelle small and slightly elongate. Antenna with 20 or 21 articles. Thoracic spines weakly developed. Mandibles (Fig. 18) very similar to those of *S. wheeleri*, with wide molar plate. Gut similar to that of *S. wheeleri*, but major midgut prolongation of mixed segment is smaller, and minor prolongation is longer and tongue shaped.

Measurements (in mm) of 20 large workers from 20 colonies: length of head 2.85-3.40; maximum width of head 3.40-3.90; length of fontanelle 0.25-0.40; width of pronotum 2.15-2.70; width of metanotum 2.30-2.90; length of hind tibia 4.40-5.50.

Comparisons. The most similar imagoes are those of *S. magnoculus* and *S. obtusus*, of which the former seems to be indistinguishable from *S. grandis*. The imago of *S. obtusus* has conspicuously larger eyes and elongate fontanelle. The soldier of *S. magnoculus* is similar, but larger and with larger marginal teeth on both mandibles and apical cutting edge not sigmoid. The soldier of *S. wheeleri* is also similar and may be sometimes difficult to distinguish from *S. grandis*. It is smaller, with sides of head more parallel, straighter mandibles with smaller marginal teeth, and more numerous hairs on head.

Distribution and Geographical Variation. This species shows a considerable morphological variation among different regions. It occurs in the cerrado of central and southeastern Brazil and in the various Amazonian savannas, including the Guianas (Fig. 321). The variation seems to be continuous and I was not able to find any consistent character that could support the distinction between *S. grandis*, *S. hageni* and *S. lighti*. They seem to be part of the same continuum, and a large series collected by A. Mathews in Mato Grosso contains different soldiers that could be identified as all three species based on Emerson's descriptions. Soldiers from the Guianas, Venezuela, and most Amazonian savannas have the sides of the head more strongly converging towards the front, the apical cutting edge of both mandibles more conspicuously sigmoid and hooked at the tip, and smaller thoracic spines (Figs. 137-141). Specimens from central and southeastern Brazil tend to have larger thoracic spines and the sides of the head converging slightly (Figs. 142-146). Soldiers from the caatinga region of northeastern Brazil have a less sigmoid apical cutting edge on both mandibles. Some populations from isolated patches of Amazonian savanna show some morphological differentiation, but collections in those areas are still very limited and the patterns are not very clear. Soldiers from Humaitá, for instance, have mandibles with larger teeth.



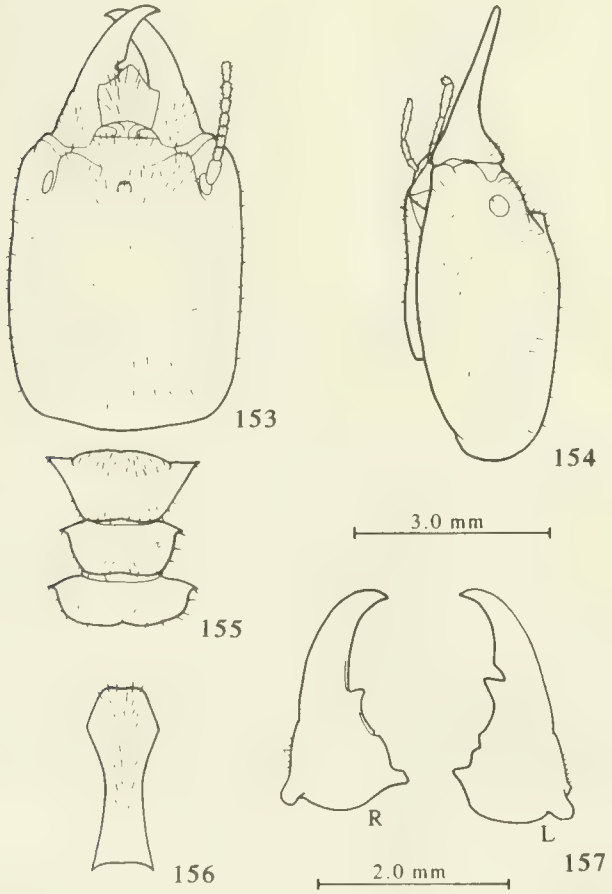
Figs. 147-152. *Syntermes grandis*. Imago: 147. head, dorsal view; 148. head, lateral view; 149. pronotum. Large worker: 150. head, dorsal view; 151. head, lateral view; 152. thorax.

Biology. *S. grandis* lives exclusively in grasslands and savannas. Its nest is mostly subterranean, with a small epigeal portion of soft consistency. According to Baker et al. (1981) the soldier defensive secretion of this species lacks terpenes, in contrast to all other examined species of the genus.

Remarks. Emerson (1945) recorded *S. lighti* from a locality named Caiçara, which he incorrectly identified as being on the Amazon. That locality, sometimes also mentioned as Caissara, was an old cattle ranch on the Paraguai River, where Natterer, the famous Austrian collector, spent one year (Araujo, 1958: 219). Natterer's specimens were studied by Hagen (1858: 156), who identified them as *T. dirus*. *S. hageni* was described from a single pinned soldier from Hagen's collection, with locality information limited to "Brazil". The type soldier of *S. hageni* is very similar to the paratypes of *S. lighti* from Caiçara, and it is likely that it was also collected by Natterer at that locality. Araujo (1977: 53), based exclusively on the literature and the study of non-type material, concluded that *S. hageni* was synonymous with *S. dirus*, and incorrectly mentioned the type locality of *S. hageni* as being Rio de Janeiro, Brazil, and the type depository as the Carnegie Museum. Apparently he arrived at that conclusion based on an erroneous redescription of *S. hageni* presented by Snyder (1924: 28), based on a misidentified specimen of *S. dirus*, and not on any type material. Snyder's mistake has already been pointed out by Emerson (1945: 461).

Syntermes insidians Silvestri

Syntermes insidians Silvestri 1946: 12 [soldier, worker]. Lectotype soldier, here designated: BRAZIL. *São Paulo*. Pitangueira (near Guarani), coll. J.P. da Fonseca, 1937 [LEFS]. Paralectotypes: one soldier, workers, same data as lectotype [AMNH], workers, same data as lectotype [LEFS].



Figs. 153-157. *Syntermes insidians*, soldier from Minas Gerais. 153. head, dorsal view; 154. head, lateral view; 155. thorax, dorsal view; 156. postmentum; 157. mandibles, ventral view.

Material examined. BRAZIL: *Mato Grosso*. Chapada dos Guimarães, coll. M.A. Drumond, 01.xii.84, soldiers [UFG-143 and 145; MZSP-9890, 9891 and 9892]; coll. E.E.B., 02.xii.84, soldiers, workers [MZSP-9895]; coll. J. Dalponte, 28.ii.88, soldiers, workers [MZSP-9911]; coll. J. Dalponte, 04.xi.84, soldiers, workers [MZSP-9912]. *Mato Grosso do Sul*. Três Lagoas, coll. C. Flechtmann, 5.iii.93, one soldier [MZSP-9829]. *Minas Gerais*. Bom Despacho, soldiers, workers [MZSP-7375]; coll. E. Vilela, 22.vi.77, soldiers, workers [MZSP-9760].

Imago. Unknown.

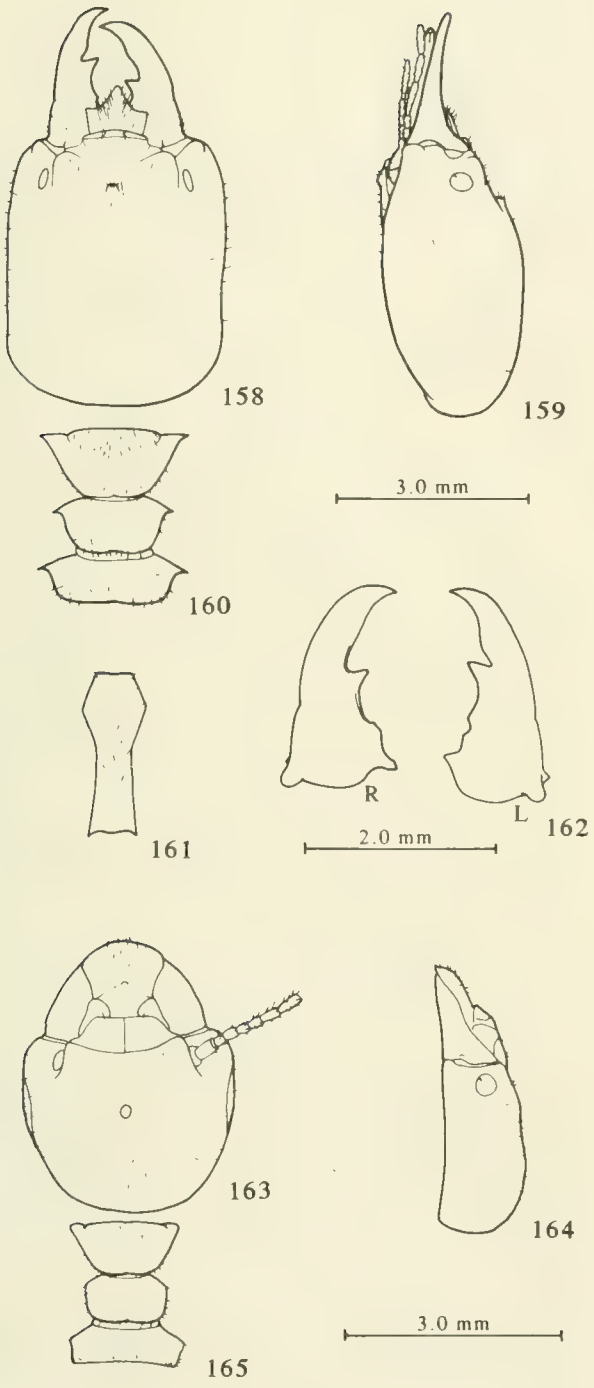
Soldier (Figs. 153-162). Head capsule elongate with parallel sides; posterior margin of head rounded; frontal tube prominent, sometimes in a small depression; pore not visible in dorsal view; labrum moderately elongate; lateral corners of labrum about equal to a right angle; median lobe of labrum elongate, longer than lateral lobes. Antenna with 20 or 21 articles. Postmentum constricted near the middle. Mandibles curved and moderately elongate; tip slightly hooked; first marginal tooth of left mandible near the middle and large, extending well beyond apical cutting edge; first marginal tooth of right mandible conspicuous; angle between right M1 and apical cutting edge less than 90°; apical cutting edge of left mandible conspicuously sigmoid, forming a notch anterior to M1; apical cutting edge of right mandible evenly curved or nearly straight with curved tip. Anterior margin of pronotum nearly rounded to slightly emarginate; posterior margin of pronotum slightly emarginate; thoracic spines weakly developed and slightly upturned, located anteriorly; lateral corners of pronotum sharp but not forming conical spines. Head capsule with numerous short, straight bristles, more numerous laterally; base of mandibles with numerous short hairs; postmentum with many short, straight bristles; pronotum with many bristles on anterior lobe and margins; meso- and metanotum with numerous bristles on posterior margin and a few on lateral margins; tergites with numerous bristles on posterior half.

Measurements (in mm) of 5 soldiers from 4 colonies: length of head 4.50-4.80; maximum width of head 3.55-3.80; height of head excluding postmentum 2.25-2.40; length of frontal tube 0.17-0.22; length of left mandible 2.20-2.35; curvature of left mandible 0.55-1.00; distance from M1 to M2 on left mandible 0.50-0.60; width of left mandible 0.60-0.64; length of left M1 0.17-0.21; minimum width of postmentum 0.59-0.76; width of pronotum 2.38-2.60; width of metanotum 2.35-2.45; length of hind tibia 3.95-4.10. Ratio length of head to maximum width of head 1.22-1.32; length of left mandible to length of head 0.47-0.51; length of hind tibia to length of head 0.84-0.88; width of pronotum to maximum width of head 0.64-0.71; distance M1-M2 to length of left mandible 0.22-0.27; height of head to maximum width of head 0.63-0.66; width to length of left mandible 0.26-0.28.

Worker (Figs. 163-165). Head capsule with many short, straight bristles. Postclypeus with four bristles. Fontanelle small and slightly elongate. Antenna with 20 or 21 articles. Thoracic nota with angular sides but lacking distinct spines. Mandibles with narrow molar plate and well marked basal notch of about 90°. Gut similar to that of *S. dirus*, but major mesenteric prolongation of mixed segment is wider and minor prolongation is more transversely elongate.

Measurements (in mm) of 5 large workers from 4 colonies: length of head 2.50-2.65; maximum width of head 2.90-3.15; length of fontanelle 0.12-0.17; width of pronotum 1.55-1.80; width of metanotum 1.55-1.85; length of hind tibia 3.65-4.05.

Comparisons. The soldier of *S. insidians* can be distinguished based on its elongate head with parallel sides, thoracic spines weakly developed and situated anteriorly, and marginal teeth well developed on both mandibles. *S. longiceps* is superficially similar, but has antenna with only 19 articles, more robust mandibles with smaller marginal teeth, larger thoracic spines, and a quite different geographic distribution.



Figs. 158-162. *Syntermes insidians*, soldier from Mato Grosso. 158. head, dorsal view; 159. head, lateral view; 160. thorax, dorsal view; 161. postmentum; 162. mandibles, ventral view.

Figs. 163-165. *Syntermes insidians*. Large worker: 163. head, dorsal view; 164. head, lateral view; 165. thorax.

Distribution and Geographical Variation. Known from a few localities in central and southeastern Brazil (Fig. 324). Specimens from Chapada dos Guimarães are a little smaller, with less numerous hairs on the head, and frontal tube in a small depression.

Biology. Seems to be associated with a particular kind of cerrado on very poor, sandy soils (Fonseca 1949, and field notes from J. Dalponte), where it may be abundant. Apparently the nest is completely subterranean. Reported as a pest of *Eucalyptus* in several locations.

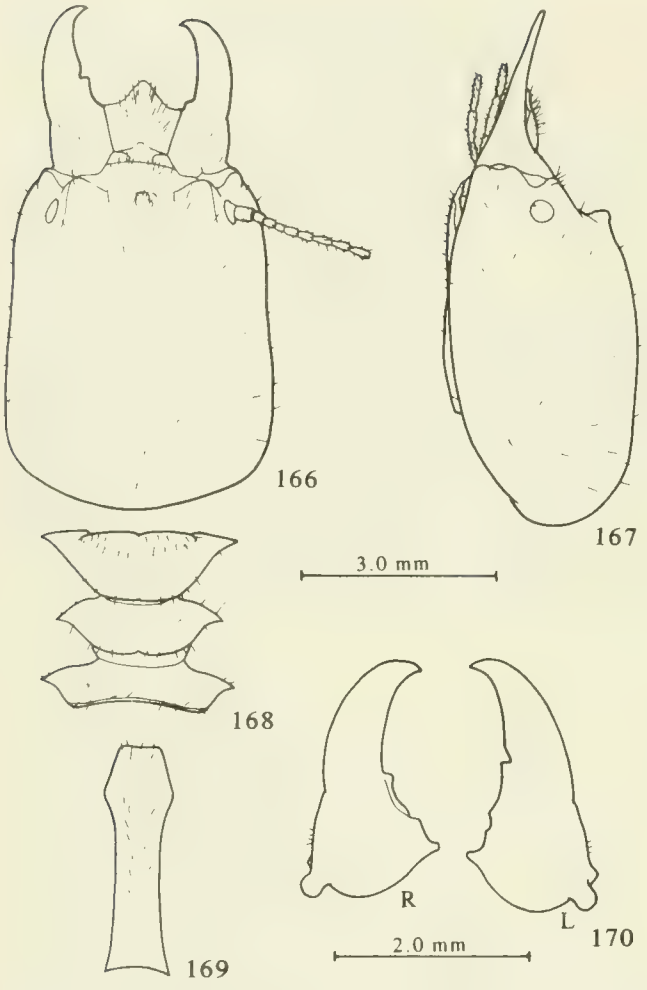
Syntermes longiceps, new species

Holotype soldier: BRAZIL. *Roraima*. S. Luís do Guará, coll. P.E. Vanzolini, 07.ii.90 [MZSP-9340]. Paratypes: No label, soldiers, alates [BMNH]. "Amaz." (probably Amazonia), coll. Saunders, one soldier [BMNH]. BRAZIL. *Amazonas*. Manaus: Reserva Ducke, coll. F.B. Apolinário, 7.viii.90, one soldier, workers [INPA-891]; coll. F.B. Apolinário, 15.i.91, soldiers, workers [INPA-892; INPA-893 and INPA-894]; coll. W. Paarman, 17.vi.92, one alate [INPA]. Manaus: INPA, coll. C. Martius, 20.iv.91, one alate [INPA]. Silves: Fazenda Aruanã, coll. A.G. Bandeira, 23.v.77, one soldier, workers [MPEG-161]. *Pará*. Benevides: Fazenda Morelândia, coll. R.B. Neto, 17.ix.80, one soldier, workers [MPEG-988]. Óbidos, coll. E.E. Austen, 2.ii.1896, alates [BMNH]. Tucuruí: Arapari, coll. W.L. Overal, 03.iii.84, soldiers, workers [MPEG-1947]. *Roraima*. S. Luís do Guará, coll. P.E. Vanzolini, 07.ii.90, one soldier, workers, same colony as holotype [MZSP-9340].

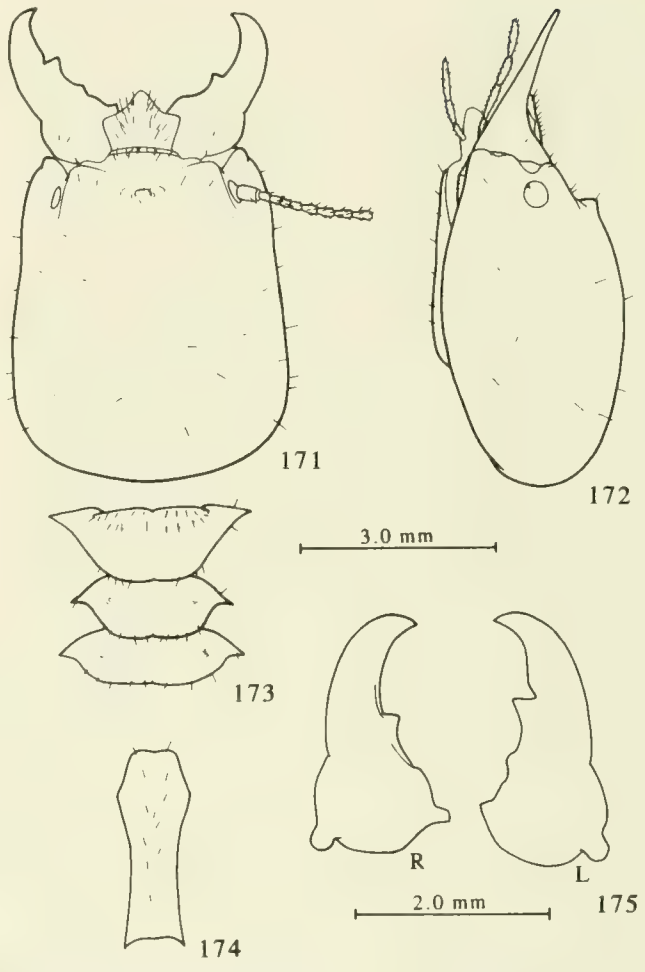
Imago (Figs. 176-178). Eyes small, less than 1/4 width of head; ocelli relatively large; fontanelle large and rounded. Antenna broken in all specimens available. Anterior corners of pronotum angular, with sharp points; lateral margins straight and nearly parallel in anterior half. Wings short (Fig. 7); distal part of media and cubitus conspicuous. Head capsule with scattered short, straight hairs; postclypeus with two short hairs on anterior margin; pronotum with many hairs on outer margin; tergites with a line of hairs on posterior margin. Head, pronotum and tergites chestnut-brown; sternites brownish yellow; wings brown to dark brown.

Measurements (in mm) of 2 imagoes from one colony: length of head 2.25-2.35; width of head without eyes 2.70-2.80; length of fontanelle 0.32-0.35; length of pronotum 1.65-1.70; width of pronotum 2.90-3.00; length of hind tibia 4.50; maximum diameter of eye 0.59-0.60; length of ocellus 0.30-0.34; length of forewing 23.00; width of forewing 1.03-1.03. Ratios: diameter of eye to width of head 0.21-0.22; length of ocellus to width of head 0.11-0.13; length of fontanelle to width of head 0.11-0.13; width of pronotum to width of head 1.04-1.11; length of wing to width of head 8.21-8.21; length of hind tibia to width of head 1.61-1.67.

Soldier (Figs. 166-175). Head capsule elongate with parallel sides; posterior margin of head rounded; frontal tube prominent, pore not visible in dorsal view; labrum short, length about equal to width; lateral corners of labrum about equal to a right angle; median lobe of labrum elongate, longer than lateral lobes. Antenna with 19 articles. Postmentum elongate and not constricted, sides of posterior part nearly parallel. Mandibles curved and moderately robust; tip slightly hooked; first marginal tooth of left mandible variable: small, not extending much beyond apical cutting edge to large, extending well beyond the apical cutting edge; first marginal tooth of right mandible conspicuous and also variable; angle between right M1 and apical cutting edge more than 90°; apical cutting edge of left mandible conspicuously sigmoid, forming a notch anterior to M1; apical cutting edge of right mandible evenly curved. Anterior margin of pronotum nearly rounded to slightly emarginate; posterior margin of pronotum nearly straight; thoracic spines weakly developed and slightly upturned; lateral corners of pronotum sharp but not forming conical spines. Head capsule with scattered straight bristles, more numerous laterally; base of mandibles with variable number of short hairs; postmentum with



Figs. 166-170. *Syntermes longiceps*, sp.n., soldier from Roraima. 166. head, dorsal view; 167. head, lateral view; 168. thorax, dorsal view; 169. postmentum; 170. mandibles, ventral view.



Figs. 171-175. *Syntermes longiceps*, sp.n., soldier from Manaus. 171. head, dorsal view; 172. head, lateral view; 173. thorax, dorsal view; 174. postmentum; 175. mandibles, ventral view.

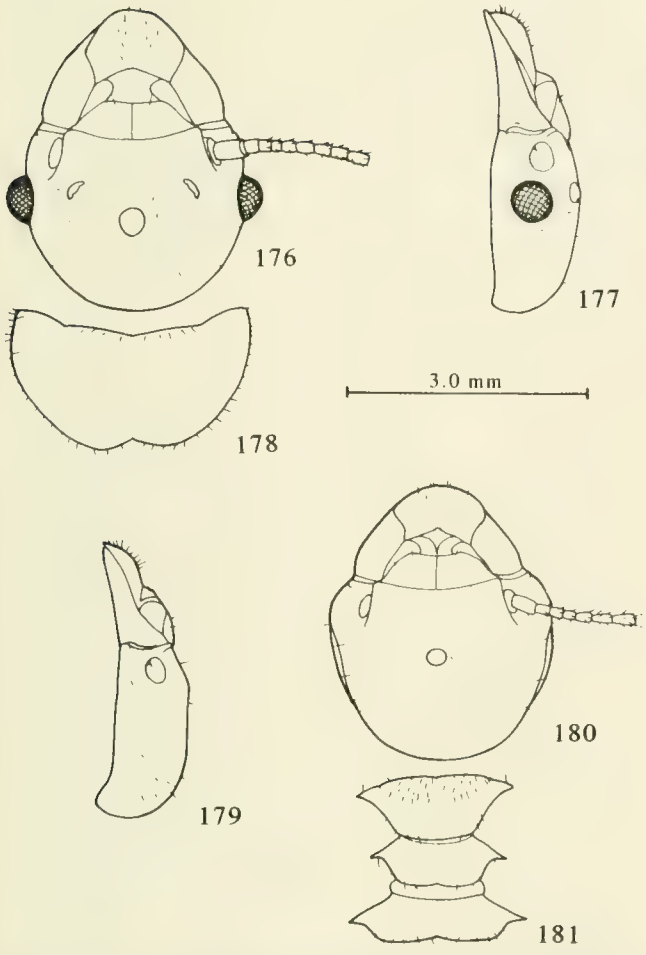
numerous short, straight bristles; pronotum with many bristles on anterior lobe and margins; meso- and metanotum with numerous bristles on posterior margin and a few on spines and lateral margins; tergites with numerous bristles on posterior half. Head pale yellow-brown; thorax pale yellow-brown; tergites and sternites yellowish, semi-transparent; legs pale yellow-brown.

Measurements (in mm) of 7 soldiers from 7 colonies: length of head 4.65-5.50; maximum width of head 3.35-4.20; height of head excluding postmentum 2.30-2.90; length of frontal tube 0.18-0.30; length of left mandible 2.05-2.45; curvature of left mandible 0.55-0.85; distance from M1 to M2 on left mandible 0.37-0.62; width of left mandible 0.62-0.76; length of left M1 0.11-0.27; minimum width of postmentum 0.69-0.81; width of pronotum 2.40-3.10; width of metanotum 2.30-3.00; length of hind tibia 3.20-3.80. Ratio length of head to maximum width of head 1.22-1.40; length of left mandible to length of head 0.42-0.51; length of hind tibia to length of head 0.67-0.72; width of pronotum to maximum width of head 0.68-0.82; distance M1-M2 to length of left mandible 0.18-0.27; height of head to maximum width of head 0.64-0.72; width to length of left mandible 0.26-0.33.

Worker (Figs. 179-181). Head capsule with scattered straight bristles. Postclypeus with about six bristles. Fontanelle rounded and small. Antenna with 19 articles. Thoracic spines weakly developed, similar to those of soldier. Mandibles (Fig. 21) with narrow molar plate and well marked basal notch of a little more than 90°. Gut distinct (Figs. 41-47), with first proctodeal segment enlarging abruptly on mixed segment; loop formed by anterior part of colon elongate; enteric valve located posteriorly; first proctodeal segment distinctly larger than paunch; major mesenteric prolongation of mixed segment relatively small, with inflated and blunt tip; minor prolongation large and tongue-shaped, touching the major one.

Measurements (in mm) of 5 large workers from 4 colonies: length of head 2.15-2.30; maximum width of head 2.65-2.80; length of fontanelle 0.18-0.22; width of pronotum 1.80-2.05; width of metanotum 1.80-2.25; length of hind tibia 3.20-3.40.

Comparisons. The alate of this species seems to be indistinguishable from that of *S. parallelus*, with both sharing the following combination of characters: small size, sharp anterior corners of pronotum, small eyes, postclypeus with only two short bristles, and dark wings. The soldier can be distinguished by its relatively small size; elongate head with parallel sides; antenna with 19 articles; thoracic spines weakly developed; and relatively short legs. It is also similar to *S. parallelus*, but is larger and the mandibles



Figs. 176-181. *Syntermes longiceps*, sp.n.. Imago: 176. head, dorsal view; 177. head, lateral view; 178. pronotum. Large worker: 179. head, dorsal view; 180. head, lateral view; 181. thorax.

are more robust and curved, with larger marginal teeth located more distally. Some of the largest soldiers of *S. longiceps* may be similar to the smallest of *S. territus*, but the latter are always larger and have small marginal teeth on both mandibles.

Distribution and Geographical Variation. Northern to northeastern Brazilian Amazonia (Fig. 324). The soldiers of this species show a large variation between different localities, but they seem to be part of the same continuum, although the material available is rather limited for a clear definition of patterns. Soldiers from the Manaus area are a little larger with conspicuously larger marginal teeth. Specimens from Pará are smaller, but otherwise identical to the type. It may be possible that there is more than one species involved here, and more collecting and field observations are necessary for a better characterization of this species. Apparently *S. longiceps* is the sister species of *S. parallelus*, which has a more northern distribution.

Biology. No information available. Certainly a forest species; nest probably completely subterranean.

Syntermes magnoculus Snyder

Syntermes magnoculus Snyder 1924: 22 [imago, soldier]; Emerson 1945: 445 [redescription]. Holotype imago female: BRAZIL. *Mato Grosso*. Chapada dos Guimarães, coll. H.H. Smith, Oct., [MCZ]. Paratypes: One alate male, same data as holotype [USNM]; one soldier, same locality and collector, but collected in "July" [MCZ].

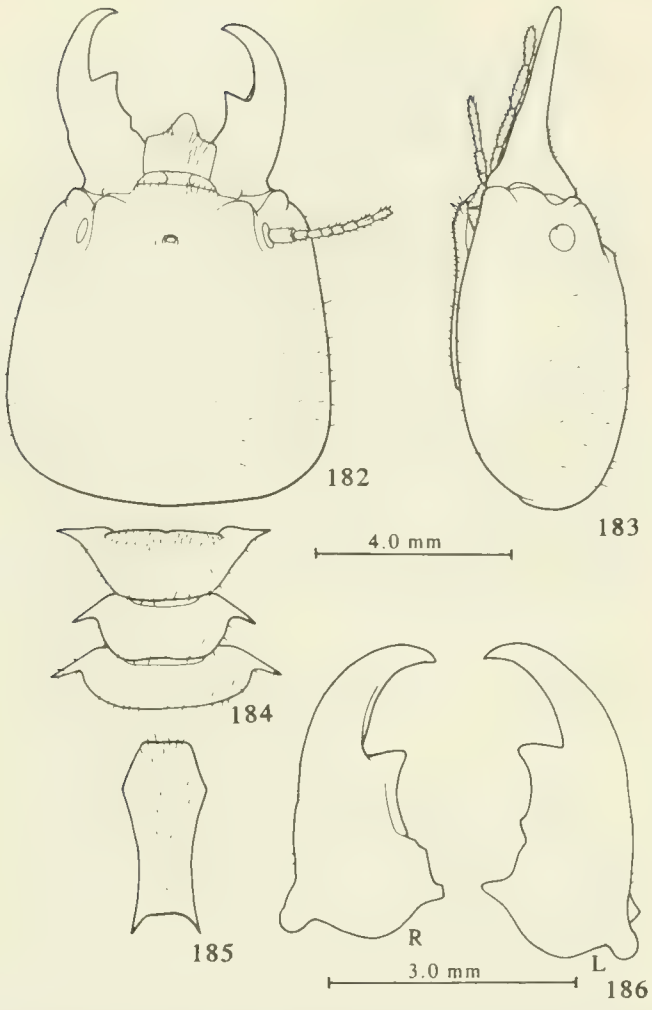
Material examined. BRAZIL. *Goiás*. Padre Bernardo, coll. H.R. Coles, 14.vii.77, soldiers, workers [MPEG-2714]; coll. H.R. Coles, 30.xii.76, soldiers [MZSP-9298]. Senador Canedo, coll. D. Brandão, 01.vi.83, soldiers, workers [UFG-63]. *Mato Grosso*. Chapada dos Guimarães, coll. R.L. Araujo, 12.ii.76, soldiers, workers [MZSP 6511]; coll. R.L. Araujo, 7.ii.76, soldiers, workers [MZSP-6506].

Imago (Figs. 187-189). Eyes large, more than 1/3 width of head; ocelli large; fontanelle rounded and relatively small. Antenna with 20 articles. Anterior corners of pronotum moderately angular; lateral margins of pronotum straight and nearly parallel in anterior half. Wings long; distal part of media and cubitus inconspicuous. Head capsule and postclypeus with numerous long bristles (many lost in type specimen); pronotum with many hairs on outer margin and surface; tergites with many hairs from middle to posterior margin. Head, pronotum, and tergites dark brown; sternites light chestnut; wings hyaline, except for brownish proximal and costal areas.

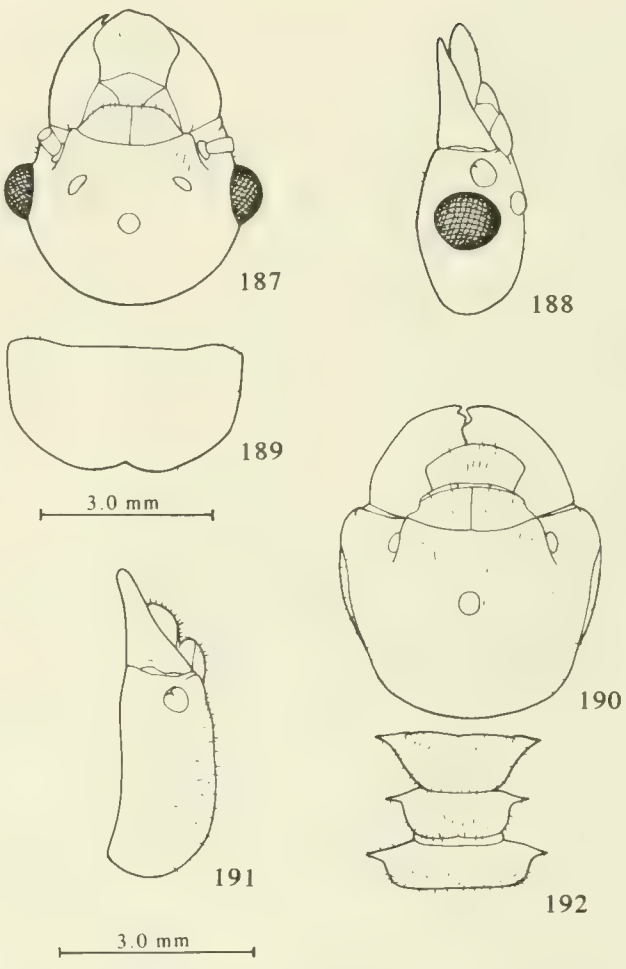
Measurements (in mm) of the holotype female: length of head to base of mandibles 3.2; width of head 3.47; length of fontanelle 0.33; length of pronotum 2.27; width of pronotum 4.2; length of hind tibia 5.2; maximum diameter of eye 1.2; length of ocellus 0.4.

Soldier (Figs. 182-186). Head capsule short, length and width of head about equal; sides converging towards front; posterior margin of head rounded; frontal tube very short, pore clearly visible in dorsal view; labrum short, length about equal to width; lateral corners of labrum about equal to or a little more than a right angle; median lobe of labrum moderately large, length about equal to lateral lobes. Antenna with 21 articles. Postmentum not constricted, sides of posterior part nearly parallel; mandibles curved and moderately elongate; tip of mandibles slightly hooked; first marginal tooth of both mandibles large, extending well beyond apical cutting edge; angle between marginal teeth and apical cutting edge less than 90°; apical cutting edge of both mandibles about evenly curved. Anterior margin of pronotum slightly emarginate; posterior margin nearly straight; thoracic spines moderately developed and strongly upturned; lateral corners of pronotum sharp but usually not forming conical spines or forming short one. Head capsule with many short, straight bristles, more numerous laterally; base of mandibles with numerous short hairs; postmentum with numerous short, straight bristles; pronotum with many bristles on entire surface, more numerous on anterior lobe; meso- and metanotum with numerous bristles on posterior margin and a few on spines and lateral margins; tergites with numerous bristles on posterior half.

Measurements (in mm) of 4 soldiers from 4 colonies: length of head 6.10-6.70; maximum width of head 6.30-7.00; height of head excluding postmentum 3.40-3.70; length of frontal tube 0.17-0.25; length of left mandible 3.20-3.70; curvature of left mandible 1.40-1.90; distance from M1 to M2 on left mandible 0.97-0.97; width of left mandible 0.97-1.24; length of left M1 0.40-0.52; minimum width of postmentum 0.87-1.08; width of pronotum 4.10-4.60; width of metanotum 4.30-4.90; length of hind tibia 5.80-6.70. Ratio length of head to maximum width of head 0.96-1.05; length of left mandible to length of head 0.51-0.55; length of hind tibia to length of head 0.91-1.00; width of pronotum to maximum width of head 0.60-0.71; distance M1-M2 to length of left mandible 0.28-0.28; height of head to maximum width of head 0.53-0.56; width to length of left mandible 0.30-0.35.



Figs. 182-186. *Syntermes magnoculus*, soldier. 182. head, dorsal view; 183. head, lateral view; 184. thorax, dorsal view; 185. postmentum; 186. mandibles, ventral view.



Figs. 187-192. *Syntermes magnoculus*. Holotype imago: 187. head, dorsal view; 188. head, lateral view; 189. pronotum. Large worker: 190. head, dorsal view; 191. head, lateral view; 192. thorax.

Worker (Figs. 190-192). Head capsule with numerous short, straight bristles. Postclypeus with about 10 bristles. Fontanelle slightly elongate and relatively small. Thoracic spines weakly developed. Mandibles and gut very similar to those of *S. grandis*, with wide molar plate on right mandible.

Measurements (in mm) of 2 large workers from 2 colonies: length of head 3.35-3.40; maximum width of head 3.95-4.00; length of fontanelle 0.37-0.39; width of pronotum 2.65-2.75; width of metanotum 2.70-2.80; length of hind tibia 4.85-5.10.

Comparisons. The alate is apparently indistinguishable from that of *S. grandis*. The soldier can be differentiated by its large size, mandibles with large marginal teeth and evenly curved apical cutting edge, and relatively short thoracic spines.

Distribution and Geographical Variation. Known from a few localities in Central Brazil (Fig. 319). Specimens from Goiás have smaller marginal teeth on both mandibles, but material is too limited to recognize any geographic pattern.

Biology. *S. magnoculus* is a cerrado species. No information about nest is available; probably completely subterranean.

Remarks. The fact that Snyder (1924) described this species from alates and soldiers collected separately poses a difficult taxonomic question. Without new material with soldiers and imagoes from the same colony, it is impossible to tell whether they really belong to the same species. Even if such material becomes available, it may be still impossible to solve the problem because alates of different species are sometimes indistinguishable, and the type is an old pinned specimen in imperfect condition. Soldiers from some samples are partially intermediate between *S. grandis* and *S. magnoculus*, and, given the similarity of alates and workers, the study of larger series might eventually show that they are just variations of the same species.

Syntermes molestus (Burmeister)

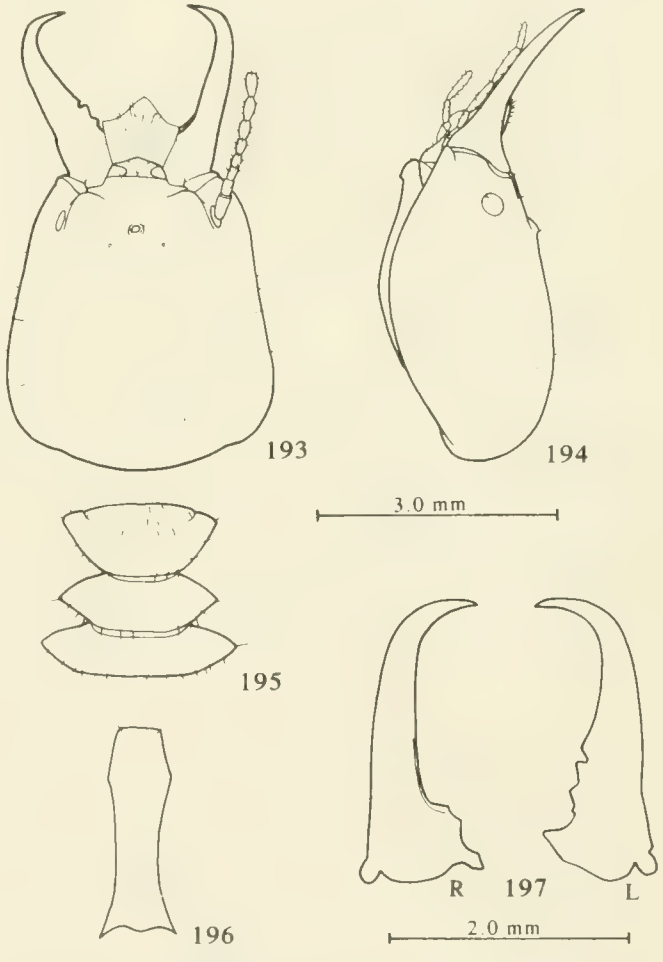
Termes molestus Burmeister 1839: 766 [imago]. Lectotype alate female, here designated: BRAZIL, *Bahia*, Coll. Gomez, pinned, [ZMHU]. Paralectotype alate female: same data as lectotype [ZMHU].

Syntermes molestus, Holmgren 1911: 547 [key]. Emerson 1945: 467 [part].

Syntermes brasiliensis Holmgren 1911: 548 [soldier, in key]. Lectotype soldier, here designated: Brazil, no data, "Syntermes n.sp." [AMNH]. Synonymized by Emerson (1945).

Material examined. BOLIVIA. *Chuquisaca.* Tumupasa, coll. W.M. Mann, xii.1921, soldiers, workers [AMNH]. BRAZIL. *Amapa.* Macapá, coll. A.L. Henriques, 21.v.89, soldiers, workers [MPEG-3109]; coll. R. Constantino, 28.x.89, soldiers, workers [MPEG-3238]. Mazagão, coll. R. Constantino, 20.x.89, soldiers, workers [MPEG-3194]. *Amazonas.* Anavilhanas, coll. A.E.Mill, 23.iv.81, soldiers, workers [BMNH]; coll. G.R. Kloss, 20.iv.67, soldiers, workers [MZSP-1804]. E. Benjamin Constant, coll. T.C.S. Pires, 08.xii.89, soldiers, workers [MPEG-3304]. Humaitá, coll. R. Constantino, 15.ix.90, one soldier, one worker [MPEG-3730]; coll. R. Constantino, 17.ix.90, soldiers, workers [MPEG-3742 and 3747]. Manaus, coll. A.G. Bandeira, 17.viii.76, soldiers, workers [MPEG-5]; coll. R.S. Bradley, 18.ix.78, soldiers, workers [MPEG-494]; coll. Og Souza, 30.vii.86, soldiers, workers [MEUV]; coll. A.G. Bandeira, 06.vi.81, soldiers, workers [MPEG-1343]; coll. S.A. Marques, 05.viii.80, soldiers, workers [MPEG-1426 and 1427]; coll. E.N. Palheta, 05.iv.91, soldiers, workers [MZSP-9472]; coll. A.G. Bandeira, 06.iv.79, soldiers, workers [MPEG-610]; coll. Og Souza, 6.viii.86, soldiers, workers [MEUV]. Maués, coll. Flavio, 06.vi.57, soldiers [MZSP-9341]. Nova Olinda, coll. E.P.A., 20.ii.72, soldiers, one worker [MZSP-5434]. Porto Urucu: Rio Urucu, coll. T.C.S. Pires, 19.xi.89, soldiers, workers [MPEG-3300]. Silves: Fazenda Aruanã, coll. A.G. Bandeira, 21.v.77, soldiers, workers [MPEG-135]. *Bahia* Coll. G. Bondar, 1925, soldiers, one worker, alates [MZSP-1844]. Andaraí, coll. E.M. Cancello, 13.xii.90, soldiers, workers [MZSP-9738]; coll. E.M. Cancello, 13.xii.90, two alates [MZSP-9737 and MZSP-9739]. Itaberaba, coll. E.M. Cancello, xii.90, soldiers [MZSP-9741]. Itaité, coll. E.M. Cancello, 18.i.80, soldiers, workers [MZSP-7917]; coll. E.M. Cancello, 13.i.80, soldiers, workers [MZSP-7918 and MZSP-7916]; coll. E.M. Cancello, 13.i.80, one alate [MZSP-7968]. Jacobina, coll. E.M. Cancello, 16.x.80, soldiers, workers [MZSP-7908]. Maracas, coll. E.M. Cancello, 24.xii.90, soldiers, workers [MZSP-9740 and MZSP-9742]. Marambaia, coll. C. Schofield, 30.iv.77, soldiers, workers [BMNH]. Sta. Rita de Cassia, coll. C.R.F. Brandão, 18.vii.91, soldiers, workers [MZSP-9733]. *Distrito Federal.* Brasília, coll. H.R. Coles, 14.ix.79, soldiers, workers [BMNH]. *Goiás.* Anápolis, coll. W.W. Kempf, 12.ii.58, soldiers [MZSP-1857]; coll. C.R. Gonçalves, 06.iii.43, soldiers, workers [MZSP-4663]. Goiás Velho, coll. A.E. Mill, 10.ii.80, soldiers [BMNH]. Goiânia, coll. D. Brandão, 16.iii.83, soldiers, workers [UFG-13 and 17]; coll. D. Brandão, xi.84, soldiers, workers [UFG-142]. Ilha do Bananal, coll. D. Brandão, 01.x.87, soldiers, workers [UFG-340]. Parque Nacional do Araguaia, coll. A. Raw, 15.vi.79, soldiers [BMNH]. Rio Paranã, coll. H.R. Coles, 30.i.77, soldiers, workers [BMNH]. *Maranhão.* Cajazeiras, coll. Reichardt, 17.vi.66, soldiers, workers [MZSP-1821]. Imperatriz, coll. G.M. Oliveira, 18.xii.72, soldiers, workers [MZSP-6335 and MZSP-6307]. *Mato Grosso.* Barra dos Bugres, coll. Braulio Dias, 13.viii.73, soldiers, workers [MZSP-7332]. Chapada dos Guimarães, coll. W.L. Overal, 17.xi.82, one alate [MPEG-3898]. Cuiabá, coll. J.C. Trager, 17.xii.84, soldiers [MZSP-8588]. E.E. Iquê-Juruena, coll. A.E. Mill, 13.vi.80, soldiers, workers [3 vials, BMNH]. Parque Indigena do Xingu, coll. R.G. Kloss, soldiers, workers [MZSP-5292]. Utiariti, coll. K. Lenko, 03.xi.65, soldiers, workers [MZSP-1807]. Xavantina, coll. A.G.A.Mathews, 12.x.68, soldiers, workers [BMNH]. *Mato Grosso do Sul.* Três Lagoas, coll. K. Lenko, 28.v.64, soldiers, one worker [MZSP-1806]. *Minas Gerais.* Francisco Sá, coll. R.L. Araujo, 16.vii.75, soldiers [MZSP-5932]; coll. R.L. Araujo, 18.vii.75, one soldier, workers [MZSP-6140]. Montes Claros, coll. R.I. Araujo, 08.i.52, soldiers [MZSP-4329]. Paracatu, coll. T.Ivanauskas, 1931, soldiers, workers, alates [AMNH and BMNH]. Pedra Azul, coll. E.M. Cancello, 21.xi.90, one soldier, workers [MZSP-9730]. Rio Pardo, coll. R.L. Araujo, 10.i.52, soldiers [MZSP-3411]. Teófilo Otoni, coll. R.L. Araujo, 27.vi.70, soldiers, workers [MZSP-4774]; coll. R.L. Araujo, 25.xii.76, soldiers, workers [MZSP-7256]. *Pará.* Canindé, coll. R. Malkin, iv.63, soldiers [MZSP-144]. Conceição do Araguaia, coll. A.Y. Harada, 31.i.83, soldiers, one worker [MPEG-2337]. Parque Nacional da Amazônia, coll. A.G. Bandeira, 23.viii.78, soldiers, workers [MPEG-422]. Santarém, Serra do Uratinga, coll. J.R. Lopes, i.1950, soldiers, workers, alates [USNM]. Serra dos Carajas, coll. R.B. Neto, 22.x.84, soldiers, workers [MPEG-2350]; coll. A.G. Bandeira, 28.i.86, one soldier, workers [MPEG-2446]. Tucuruí, coll. A.G. Bandeira, 21.iv.79, soldiers, workers [MPEG-618]; coll. W.L. Overal, 22.vi.84, soldiers, workers [MPEG-2273]. *Rio de Janeiro.* Rio de Janeiro, coll. J. Smith, one soldier [BMNH]. *Rondônia.* 1985, soldiers, workers [MPEG-3920, MPEG-3921 MPEG-3922]. Ouro Preto do Oeste, coll. F. Ramos, 26.iii.85, soldiers, workers [MPEG-2287]; coll. R.B. Neto, 26.iii.85, soldiers, workers [MPEG-2286]; coll. J.O. Dias, 26.iii.85, soldiers [MPEG-2288]. *Roraima.* Ilha de Maracá, coll. A.G. Bandeira, 23.ii.88, soldiers, workers [INPA-673]; coll. Carmozing, 13.v.88, soldiers, workers [MZSP-9471]; coll. A.G. Bandeira, 04.ii.88, one soldier, workers [INPA-382 and INPA-425]; coll. S. Ferraz, 16.ii.88, soldiers, workers [INPA-763]; coll. A.G. Bandeira, 21.xi.78, soldiers, workers [MPEG-3467]. Vista Alegre, Rio Branco, coll. J. Bequaert, 6.ix.24, soldiers, workers [AMNH]. *São Paulo.* São Paulo, one soldier, one worker [BMNH]. COLOMBIA. Meta. Villavicencio, coll. C.H. Seevers, 16.vii.38, soldiers, workers, queen and king [AMNH].

Imago (Figs. 198-200). Eyes moderately large, more than 1/4 width of head; ocelli large; fontanelle rounded and large. Antenna with 20 articles. Anterior corners of pronotum rounded; lateral margins rounded and converging posteriorly. Wings long; distal



Figs. 193-197. *Syntermes molestus*, soldier. 193. head, dorsal view; 194. head, lateral view; 195. thorax, dorsal view; 196. postmentum; 197. mandibles, ventral view.

part of media and cubitus inconspicuous. Head capsule with numerous long bristles; postclypeus with two bristles on anterior margin and two near middle; pronotum with many hairs on outer margin and only a few scattered ones on surface; tergites with a line of hairs on posterior margin. Head and pronotum light chestnut; tergites chestnut-brown; sternites brownish yellow; wings hyaline, except for brownish proximal and costal areas.

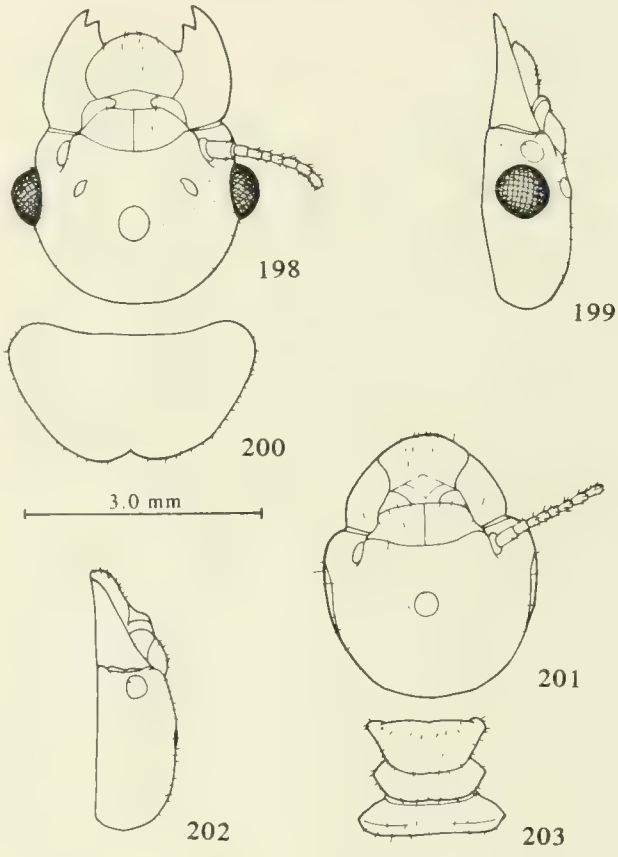
Measurements (in mm) of 5 imagoes from 5 colonies: length of head 2.15-2.25; width of head without eyes 2.35-2.55; length of fontanelle 0.34-0.45; length of pronotum 1.60-1.75; width of pronotum 2.95-3.05; length of hind tibia 4.00-4.50; maximum diameter of eye 0.69-0.81; length of ocellus 0.27-0.34; length of forewing 22.00-26.50; width of forewing 6.00-7.00. Ratios: diameter of eye to width of head 0.28-0.32; length of ocellus to width of head 0.11-0.13; length of fontanelle to width of head 0.13-0.18; width of pronotum to width of head 1.18-1.26; length of wing to width of head 9.36-10.39; length of hind tibia to width of head 1.60-1.76.

Soldier (Figs. 193-197). Head capsule elongate with sides converging towards front; posterior margin of head rounded or weakly three-lobed; frontal tube very short, pore clearly visible in dorsal view; labrum short, length about equal to width; lateral corners of labrum about equal to a right angle; median lobe of labrum large. Antenna with 19 or 20 articles. Postmentum slightly constricted near the middle, usually with a pimple-like projection near anterior end. Mandibles slender and elongate; tip strongly hooked; first marginal tooth of left mandible near the base and small, not extending much beyond apical cutting edge; first marginal tooth of right mandible vestigial or absent; apical cutting edge of left mandible evenly rounded, but forming a notch anterior to M1; cutting edge of right mandible mostly straight, with evenly curved distal portion. Anterior margin of pronotum slightly emarginate; posterior margin nearly straight; thoracic spines absent, lateral margins of nota angular and not upturned. Head capsule with scattered short, straight bristles, more numerous laterally; base of mandibles without hairs; postmentum with only two straight bristles on anterior corners; pronotum with many bristles on anterior lobe and margins; meso- and metanotum with numerous bristles on posterior margin and a few on lateral margins; tergites with many bristles near hind margin.

Measurements (in mm) of 10 soldiers from 10 colonies: length of head 3.75-4.30; maximum width of head 3.00-3.65; height of head excluding postmentum 1.80-2.25; length of frontal tube 0.03-0.08; length of left mandible 2.05-2.20; curvature of left mandible 0.70-0.98; distance from M1 to M2 on left mandible 0.17-0.25; width of left mandible 0.50-0.60; length of left M1 0.07-0.08; minimum width of postmentum 0.49-0.66; width of pronotum 1.75-2.10; width of metanotum 2.20-2.65; length of hind tibia 3.30-3.80. Ratio length of head to maximum width of head 1.17-1.25; length of left mandible to length of head 0.49-0.59; length of hind tibia to length of head 0.79-0.95; width of pronotum to maximum width of head 0.53-0.60; distance M1-M2 to length of left mandible 0.08-0.12; height of head to maximum width of head 0.60-0.63; width to length of left mandible 0.23-0.29.

Large worker (Figs. 201-203). Head capsule with many short, straight bristles; postclypeus with about 14 bristles. Fontanelle rounded and relatively large. Antenna with 19 or 20 articles. Lateral margins of thoracic nota angular, but lacking spines. Mandibles similar to those of *S. nanus* (Fig. 22); left apical tooth short; cutting edge of left M1 slightly undulate; right A and M1 about the same size; molar plate narrow with well marked basal notch of about 90°. Gut (Figs. 48-53) less voluminous than in *S. dirus*; mixed segment plus first proctodeal segment broadly tubular, without any abrupt enlargement; major midgut prolongation of mixed segment elongate, with conspicuously inflated distal portion; minor prolongation tongue-shaped and relatively large, touching the major prolongation.

Measurements (in mm) of 4 large workers from 4 colonies: length of head 2.00-2.15; maximum width of head 2.45-2.60; length of fontanelle 0.20-0.27; width of pronotum 1.35-1.53; width of metanotum 1.65-1.80; length of hind tibia 2.60-2.85.



Figs. 198-203. *Syntermes molestus*. Imago: 198. head, dorsal view; 199. head, lateral view; 200. pronotum. Large worker: 201. head, dorsal view; 202. head, lateral view; 203. thorax.

Comparisons. All castes are close to *S. nanus* and distinct from all other species of *Syntermes*. The alate can be distinguished by its small size, large eyes, rounded corners of pronotum, long and hyaline wings, and postclypeus with only four bristles. The imago of *S. nanus* is smaller and darker colored, and has a smaller fontanelle and a narrower pronotum. The soldier can be distinguished by its small size, elongate mandibles with reduced marginal dentition and strongly hooked tip, and the absence of thoracic spines. The soldier of *S. nanus* is smaller, the sides of the head are parallel, the mandibles are less hooked, and some hairs are present on the posterior part of the postmentum.

Distribution and Geographical Variation. This is the species of *Syntermes* with the widest distribution, from southeastern Brazil to Colombia and the Guianas (Fig. 322). Although there is some morphological variation, there is no clear geographic pattern, and specimens from Bahia, near the Atlantic coast, are very similar to those from Colombia.

Biology. *S. molestus* is a forest species, and its nest is completely subterranean. It may be found foraging on the forest floor even during the day, leaving the underground galleries through small circular openings.

Remarks. Many of the references about *S. molestus* in the liter-

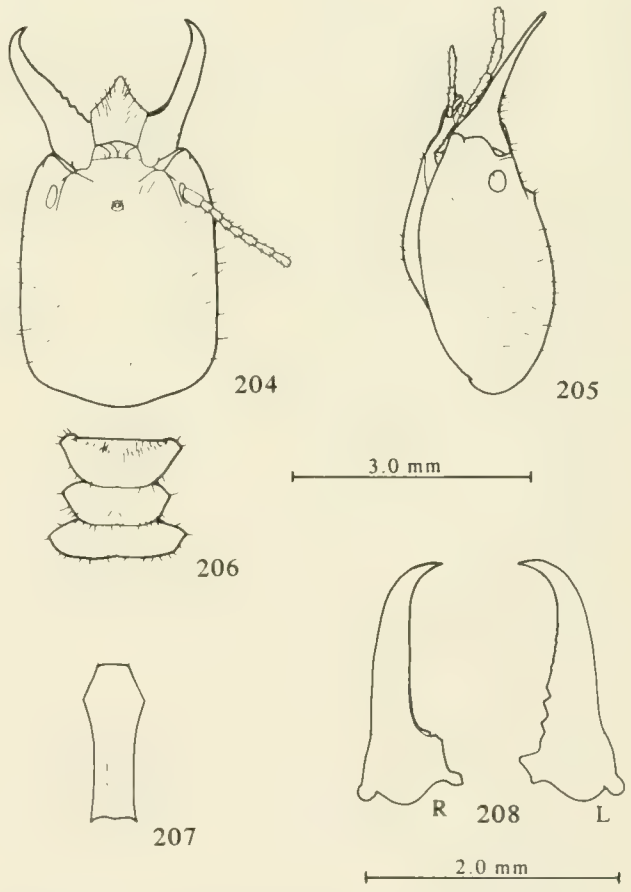
ature actually refer to *S. nanus*. Apparently, soldiers of *S. nanus* collected by Silvestri (1903) in Paraguay and Mato Grosso, erroneously determined as *S. molestus*, became reference ("morphotypes") because only the alates of *S. molestus* were previously known. Holmgren (1911) was able to distinguish the two species, but, because he used Silvestri's morphotypes for comparison, he described the true soldiers of *S. molestus* as a new species, *S. brasiliensis*. Emerson (1945) considered the two forms as variations of the same species, probably due to limited material and biological information. Although both species show considerable variation with a little overlap in some characters, their size distribution is clearly bimodal, both soldiers and imagoes are different, and there is a clear habitat separation.

Syntermes nanus, new species

Termes molestus, Silvestri 1903: 51, misidentification [part], 116 [biology]; plate II: figs. 84 [imago] and 86 [soldier].
Syntermes molestus, Emerson 1945: 467, misidentification [part].

Holotype soldier: BRAZIL. *São Paulo.* Pirassununga, coll. O. Schubart, 1954, [MZSP-4239]. Paratypes: BRAZIL. *Amazonas.* Humaitá, coll. R. Constantino, 18.ix.90, soldiers, workers [MPEG-3763]. *Bahia.* Salvador, coll. R.L. Araujo, 02.vii.70, soldiers, one worker [MZSP-4832]. *Ceará.* Crato, coll. R.L.A., 10.xi.75, one soldier, workers [MZSP-6454]. *Distrito Federal.* Brasília, coll. H.R. Coles, 14.ix.79, soldiers, workers [two vials, BMNH]; coll. A.E.Mill, 11.iii.80, soldiers, workers [BMNH]; coll. H.R. Coles, 30.iv.77, soldiers, workers [BMNH]; coll. H.R. Coles, 06.xi.76, soldiers, workers [MZSP-9300]; coll. M.G. Siqueira, 03.vi.82, soldiers, workers [two vials, UnB]; coll. M.G. Siqueira, 24.vi.82, soldiers, workers [two vials, UnB]. *Goiás.* Alvorada do Norte, coll. C.R.F. Brandão, 9.vii.91, one soldier, workers [MZSP-9731]; coll. Amarante, vii.91, soldiers, workers [MZSP-9732]. Formosa, coll. Goodland, 12.xii.65, soldiers, workers [MZSP-1169]. Goiânia, coll. R.F. Souza, 18.vii.91, one soldier, workers [UFG-439]. Parque Nacional das Emas, coll. Mill & Redford, 9.vii.80, soldiers, one worker [BMNH]. Padre Bernardo, coll. H.R. Coles, 17.xii.77, soldiers, workers [BMNH]. *Mato Grosso.* Aquidauana, coll. R.L. Araujo, 26.x.53, soldiers, workers [MZSP-3937]. Cáceres, coll. M. Zanuto, 02.iii.85, soldiers, workers [MPEG-2327]. Chapada dos Guimarães, coll. W.L. Overal, 17.xi.82, soldiers [MPEG-2742]; coll. W.L. Overal, 18.xi.82, one soldier, workers [MPEG-2774]. Coxipó, coll. R.L. Araujo, 18.ii.76, soldiers, workers [MZSP-6677]. Cuiabá, 22.xi.84, soldiers, workers [MZSP-9893]; coll. J.C. Dalponte, 11.ix.82, soldiers, workers [MPEG-3895]. Diamantino, coll. H. Reichardt, 10.viii.73, soldiers, workers [MZSP-5235]. Utiariti, coll. Lenko & Pereira, 29.xi.66, soldiers, workers [MZSP-1802]. Xavantina, coll. H.R. Coles, 01.iv.78, soldiers, workers [BMNH]; coll. H.R.Coles, 12.i.77, soldiers, workers [BMNH]; coll. A.G.A.Mathews, 18.ix.68, soldiers, workers [5 vials, BMNH]; coll. A.G.A.Mathews, 12.ii.68, one soldier, workers [BMNH]. *Mato Grosso do Sul.* Corumbá, one soldier, workers [ZMUC]; coll. F. Silvestri, 1900, one soldier, workers [ISNB]; coll. R.L. Araujo, 29.x.53, soldiers, workers [MZSP-3955 and 3959; AMNH]. Rio Paraguai, coll. G. Schaller, soldiers, workers [AMNH]; coll. G. Schaller, iv.78, soldiers [AMNH]. Três Lagoas, coll. K. Lenko, 20.v.64, soldiers, workers [MZSP-1803]; coll. F. Lane, iv.66, soldiers, workers [MZSP-1034]. *Minas Gerais.* Araxá, coll. R.L. Araujo, 10.xi.73, soldiers, workers [MZSP-5748]. Belo Horizonte, coll. R.L. Araujo, 15.i.54, soldiers, workers [MZSP-4109]; coll. R.L. Araujo, 04.i.54, soldiers [MZSP-4063]. Bom Sucesso, soldiers, workers [MZSP-7374]. Capitão Eneias, coll. R.L. Araujo, 15.vii.75, soldiers, workers [MZSP-6249]. Divinópolis, coll. O.F. Souza, 04.x.93, soldiers, workers [MEUV]. Lagoa Santa, coll. R.L. Araujo, 17.viii.71, soldiers, workers [MZSP-4951]. Montes Claros, coll. R.L. Araujo, 17.xi.72, soldiers, workers [MZSP-5834]. Tiradentes, coll. R.L. Araujo, 30.vii.75, soldiers, workers [MZSP-5962]. Uberaba, coll. R.L. Araujo, 22.iv.72, soldiers, workers [MZSP-4990]. *Paraíba.* Independencia, soldiers, workers [MZSP-1845]. *Pernambuco.* Engenho do Rio Morto, coll. B. Dantas, 06.viii.58, soldiers, workers, one alate [MZSP-4688]. *Rio Grande do Norte.* Natal, Paranamirim Field, coll. H.T. Dalmat, 26.ii.45, alates [AMNH]. *Rio de Janeiro.* S.J. da Barra, coll. M.M. Chaves, 06.ix.63, soldiers, one worker [MZSP-1823]. *Rondônia.* Vilhena, coll. A.E. Mill, 06.x.80, 3 vials with soldiers, workers and alates [BMNH]; coll. A.E. Mill, 23.vii.80, soldiers, workers [MPEG-1267]. *Sergipe.* Estância, coll. R.L. Araujo, 23.xi.75, soldiers, workers [MZSP-6452]. Sto. Amaro das Brotas, coll. F. Val, 9.ii.88, soldiers, workers [MZSP-9751]. *São Paulo.* Agudos, coll. W. Kempf, 08.v.52, soldiers, workers [MZSP-1100]. Guarani, coll. J.V. Pinheiro, ii.43, one soldier, workers [MZSP-2786]; coll. J.P. Fonseca, 06.xi.43, soldiers, workers [MZSP-2911 and 2912]; no data, soldiers, one worker [MZSP-3782]. Itirapina, coll. C.R.F. Brandão, 19.x.90, soldiers, workers [MZSP-9415]. Jacareí, coll. R.L. Araujo, 27.ii.57, soldiers, workers [MZSP-3312]. Pirassununga, coll. O. Schubart, 25.iv.53, soldiers, one worker [AMNH]; coll. O. Schubart, 1954, soldiers, workers, same colony as holotype [MZSP-4239]; coll. D. Braz, 28.ix.47, soldiers, one worker [MZSP-3064]. Ribeirão Preto, coll. M.C. Rigo, 07.vii.67, soldiers, workers [MZSP-1801]. S.J. do Rio Preto, coll. I. Watanabe, ii.72, alates [MZSP-5178]. S.J. dos Campos, coll. A. Sanches, 17.v.53, soldiers [MZSP-3846]. PARAGUAY. Monte Sociedad, coll. Ternetz, 1895, soldiers, workers [AMNH].

Imago (Figs. 209-211). Eyes very large, more than 1/3 width of head; ocelli large; fontanelle small, rounded and concave. Antenna



Figs. 204-208. *Syntermes nanus*, sp.n., soldier. 204. head, dorsal view; 205. head, lateral view; 206. thorax, dorsal view; 207. postmentum; 208. mandibles, ventral view.

with 19 or 20 articles. Anterior corners of pronotum rounded; lateral margins of pronotum rounded and converging posteriorly. Wings very long (Fig. 8); distal part of media and cubitus inconspicuous. Head capsule with numerous long hairs; postclypeus with two hairs on anterior margin and two near middle; pronotum with many hairs on outer margin and a few scattered ones on surface; tergites with a line of hairs on posterior margin. Head, pronotum, and tergites dark brown; sternites brownish yellow; wings hyaline, except for brownish proximal and costal areas.

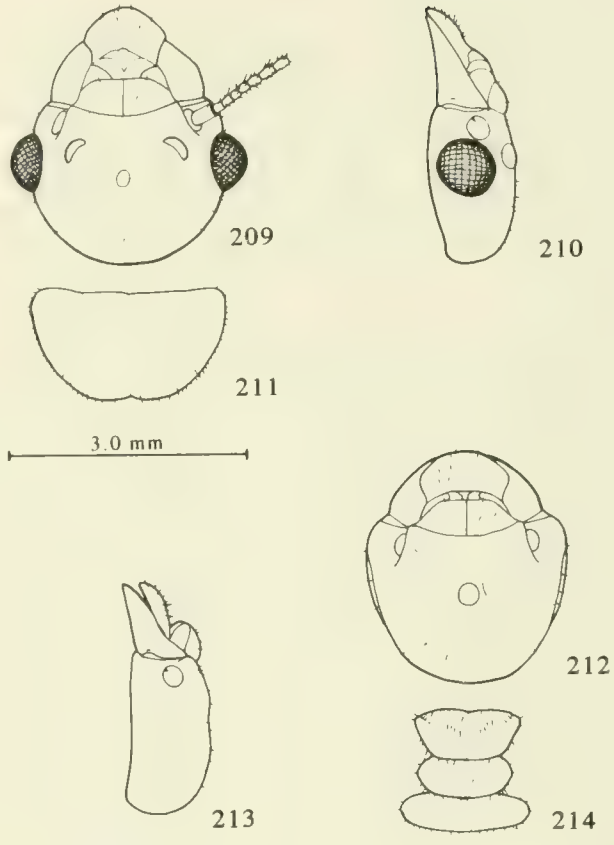
Measurements (in mm) of 6 imagoes from 5 colonies: length of head 1.90-2.10; width of head without eyes 2.15-2.40; length of fontanelle 0.17-0.34; length of pronotum 1.33-1.50; width of pronotum 2.35-2.55; length of hind tibia 3.65-4.10; maximum diameter of eye 0.76-0.82; length of ocellus 0.30-0.40; length of forewing 24.50-26.00; width of forewing 6.20-6.40. Ratios: diameter of eye to width of head 0.32-0.38; length of ocellus to width of head 0.13-0.17; length of fontanelle to width of head 0.07-0.14; width of pronotum to width of head 1.02-1.14; length of wing to width of head 10.21-11.86; length of hind tibia to width of head 1.59-1.88.

Soldier (Figs. 204-208). Head capsule elongate with nearly parallel sides; posterior margin of head rounded or weakly three-lobed; frontal tube very short, pore clearly visible in dorsal view; labrum elongate, longer than width; lateral corners of labrum forming an obtuse angle; median lobe of labrum elongate, longer than lateral lobes. Antenna with 19 articles. Postmentum not constricted, sides of posterior part nearly parallel. Mandibles slender and elongate; tip moderately hooked; first marginal tooth of left mandible near base and small, not extending much beyond apical cutting edge; first marginal tooth of right mandible vestigial or absent; apical cutting edge of left mandible evenly rounded and finely serrated, forming a notch anterior to M1; cutting edge of right mandible straight with evenly curved tip. Anterior margin of pronotum slightly emarginate (visible in posterior view only); posterior margin of pronotum nearly straight; thoracic spines absent, lateral margins of nota angular and not upturned. Head capsule in dorsal view with numerous straight, short bristles, more numerous laterally; base of mandibles with a few hairs; postmentum with two straight bristles on anterior corners plus some on posterior part; pronotum with many bristles on anterior lobe and margins; meso- and metanotum with numerous bristles on posterior margin and a few on spines and lateral margins; tergites with numerous bristles on posterior half.

Measurements (in mm) of 11 soldiers from 11 colonies: length of head 2.85-3.65; maximum width of head 2.20-2.85; height of head excluding postmentum 1.45-1.85; length of frontal tube 0.05-0.10; length of left mandible 1.65-1.95; curvature of left mandible 0.38-0.55; distance from M1 to M2 on left mandible 0.15-0.20; width of left mandible 0.35-0.49; length of left M1 0.03-0.06; minimum width of postmentum 0.45-0.60; width of pronotum 1.35-1.60; width of metanotum 1.53-2.05; length of hind tibia 2.50-3.00. Ratio length of head to maximum width of head 1.22-1.31; length of left mandible to length of head 0.49-0.61; length of hind tibia to length of head 0.78-0.91; width of pronotum to maximum width of head 0.56-0.61; distance M1-M2 to length of left mandible 0.09-0.11; height of head to maximum width of head 0.62-0.69; width to length of left mandible 0.20-0.27.

Large worker (Figs. 212-214). Head capsule with many straight bristles; postclypeus with about six bristles. Fontanelle small and slightly elongate. Antenna with 19 or 20 articles. Thoracic nota with angular sides but lacking spines. Mandibles (Fig. 22) with left apical tooth small; cutting edge of left M1 slightly undulate; right A and M1 nearly equal; molar plate narrow, with well marked basal notch of about 90°. Gut very similar to that of *S. molestus* (Figs. 48-53).

Measurements (in mm) of 4 large workers from 4 colonies: length of head 1.90-2.10; maximum width of head 2.30-2.50; length of fontanelle 0.15-0.22; width of pronotum 1.20-1.30; width of metanotum 1.45-1.55; length of hind tibia 2.30-2.80.



Figs. 209-214. *Syntermes nanus*, sp.n.. Imago: 209. head, dorsal view; 210. head, lateral view; 211. pronotum. Large worker: 212. head, dorsal view; 213. head, lateral view; 214. thorax.

Comparisons. The closest species is *S. molestus*. The alate of *S. nanus* is smaller, darker colored, with proportionally narrower pronotum and smaller fontanelle. The soldier of *S. nanus* is smaller, with sides of head parallel, less hooked mandibles, and some bristles on posterior part of postmentum. See also comparisons under *S. molestus*.

Distribution and Geographical Variation. Most parts of Brazil except Amazonia and southernmost states; a few records in Paraguay and northern Argentina (Fig. 323). There is considerable morphological variation, but no clear geographic pattern. Soldiers from Mato Grosso do Sul seem to be a little larger.

Biology. *S. nanus* lives in savannas and grasslands, where it feeds on grasses. The nest is completely subterranean and has never been described.

Remarks. See remarks under *S. molestus*.

Syntermes obtusus Holmgren

Termes grandis, Silvestri 1903: 49, misidentification [imago, workers], 116 [biology]; plate II; fig. 79 [imago].

Syntermes obtusus Holmgren 1911: 547 [imago, in key]; Emerson 1945: 414 [redescription]. Lectotype imago male, here designated: PARAGUAY. Villa Rica, coll. F. Silvestri, 8.x.1900 [AMNH]. Paralectotypes: Four workers, same data as lectotype [AMNH]. Other syntypes not found in LEFS or NHRS.

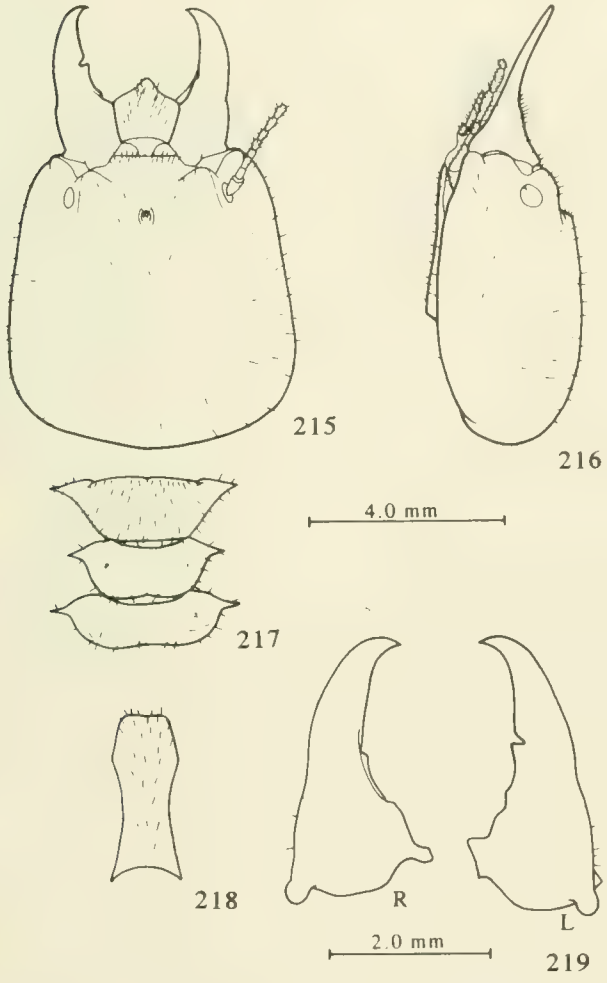
Termes dirus, Silvestri 1903: 48, misidentification [soldier, worker]; 115 [biology]; type material of *S. silvestrii*

Syntermes silvestrii Holmgren 1911: 548 [soldier]; Emerson 1945: 462 [redescription]; synonymized by Araujo 1977: 6. Lectotype soldier, here designated: BRAZIL. *Mato Grosso*. Cuiabá, coll. F. Silvestri, 6.ix.1900 [AMNH].

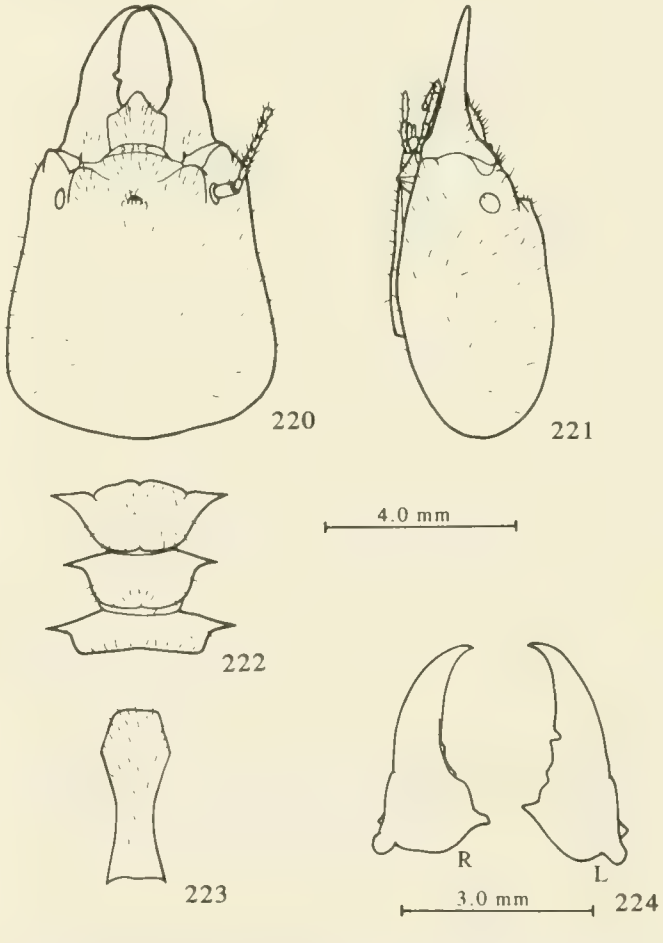
Material examined. ARGENTINA. *Corrientes*. San Miguel: San Antonio, coll. G. Torales, soldiers, workers [UNN]. *Misiones*. Loreto, coll. F. Silvestri, 27.vi.35, soldiers, workers [AMNH]; coll. Kuznesov, 20.vii.49, soldiers, workers [AMNH]; coll. Cernosvitov, soldiers, workers [BMNH]; coll. Silvestri, 28.vi.35, soldiers, workers [MZSP-1859]. Southern BOLIVIA. Coll. Hill, one soldier, one worker [AMNH]. BRAZIL. *Goias*. Parque Nacional das Emas, coll. K. Redford, ix.1981, soldiers, workers [MZSP-9781]. *Mato Grosso*. Chapada dos Guimarães, coll. M.A. Drumond, 01.xii.84, one soldier, workers [UFG-144]; coll. M.A. Drumond, 7.xii.84, soldiers, workers [MZSP-9896]. Cuiabá, coll. W.L. Overal, 19.ii.85, soldiers, workers [MPEG-2308]. Jaraguá, coll. R.L. Araujo, 24.x.53, soldiers, workers [MZSP-3927]. *Mato Grosso do Sul*. Campo Grande, coll. G. Muller, 06.vi.52, one soldier [MZSP-1868]; coll. R.I. Araujo, 25.x.53, soldiers, workers [MZSP-3924]; coll. R.L. Araujo, 20.ii.76, soldiers, workers [MZSP-6505]. *São Paulo*. Itapetininga, coll. Rabello, 09.viii.67, soldiers, workers [MZSP-1843]. Tatuí, coll. J.P. Fonseca, viii.56, soldiers, workers [MZSP-3221]. PARAGUAY. San Bernardino, coll. Fiebrig, one soldier, one worker [AMNH].

Imago (Figs. 225-227). Eyes large, more than 1/3 width of head; ocelli large; fontanelle elongate and moderately large. Antenna with 21 articles. Anterior corners of pronotum moderately angular; anterior half of lateral margins of pronotum straight and nearly parallel. Head capsule with numerous long hairs; postclypeus with many hairs; pronotum with many hairs on margins and entire surface; tergites with many hairs from middle to posterior margin. Head dark brown; pronotum chestnut-brown; tergites dark brown; sternites light chestnut; wings hyaline, except for brownish proximal and costal areas.

Measurements (in mm) of the holotype male: length of head 3.10; width of head without eyes 3.45; length of fontanelle 0.52; length of pronotum 2.50; width of pronotum 4.25; length of hind tibia 6.50; maximum diameter of eye 1.23; length of ocellus 0.45. Ratios: diameter of eye to width of head 0.36; length of ocellus to width of head 0.13; length of fontanelle to width of head 0.15; width of pronotum to width of head 1.23; length of hind tibia to width of head 1.88.



Figs. 215-219. *Syntermes obtusus*, soldier from Argentina. 215. head, dorsal view; 216. head, lateral view; 217. thorax, dorsal view; 218. postmentum; 219. mandibles, ventral view.



Figs. 220-224. *Syntermes obtusus*, soldier from Cuiabá, lectotype of *S. silvestrii*. 220. head, dorsal view; 221. head, lateral view; 222. thorax, dorsal view; 223. postmentum; 224. mandibles, ventral view.

Soldier (Figs. 215-224). Head capsule short, length and width of head about equal, sides slightly to conspicuously converging anteriorly; posterior margin of head rounded or weakly three-lobed; frontal tube short, pore clearly visible in dorsal view or a little prominent and oriented anteriorly; labrum short, length about equal to width; lateral corners forming an obtuse angle; median lobe short. Antenna with 20 or 21 articles. Postmentum constricted near the middle. Mandibles curved and moderately elongate; tip slightly hooked; first marginal tooth of left mandible small, not extending much beyond apical cutting edge; first marginal tooth of right mandible reduce or vestigial; apical cutting edge of left mandible conspicuously sigmoid, forming a notch anterior to M1; apical cutting edge of right mandible straight, except for curved tip. Anterior margin of pronotum nearly rounded to slightly emarginate; posterior margin of pronotum nearly straight; thoracic spines moderately developed and strongly upturned; lateral corners of pronotum sharp, sometimes forming short conical spines. Head capsule in dorsal view with many short, straight bristles, more numerous laterally; postclypeus densely covered with short hairs; base of mandibles with numerous short hairs; postmentum with numerous short, straight bristles; pronotum with many bristles on entire surface, more numerous on anterior lobe; meso- and metanotum with numerous bristles on posterior margin and a few on spines and lateral margins; tergites with many bristles near hind margin.

Measurements (in mm) of 8 soldiers from 8 colonies: length of head 5.60-6.50; maximum width of head 5.25-6.20; height of head excluding postmentum 2.80-3.40; length of frontal tube 0.05-0.25; length of left mandible 2.90-3.25; curvature of left mandible 0.75-1.10; distance from M1 to M2 on left mandible 0.42-0.64; width of left mandible 0.76-0.87; length of left M1 0.12-0.22; minimum width of postmentum 0.76-0.96; width of pronotum 3.40-4.20; width of metanotum 3.30-4.10; length of hind tibia 4.90-6.10. Ratio length of head to maximum width of head 0.98-1.07; length of left mandible to length of head 0.49-0.55; length of hind tibia to length of head 0.84-1.09; width of pronotum to maximum width of head 0.63-0.71; distance M1-M2 to length of left mandible 0.14-0.20; height of head to maximum width of head 0.53-0.56; width to length of left mandible 0.25-0.28.

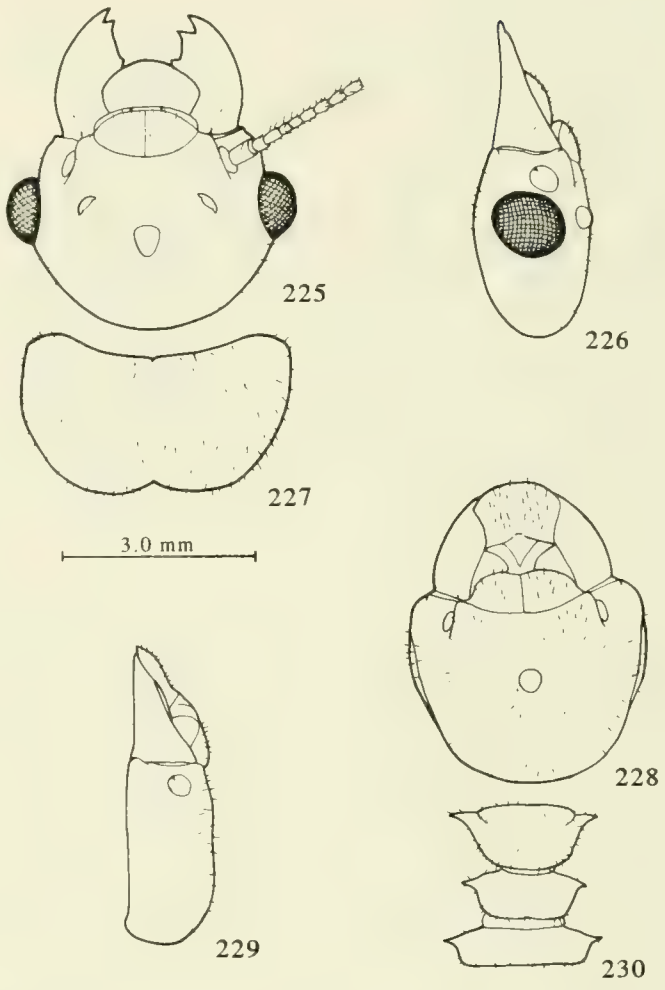
Large worker (Figs. 228-230). Head capsule covered with numerous short, straight bristles. Postclypeus with many short bristles. Fontanelle large and roughly triangular. Antenna with 20 or 21 articles. Thoracic spines moderately developed. Mandibles similar to those of *S. grandis*, with wide molar plate. Gut similar to that of *S. wheeleri*, but with major midgut prolongation of mixed segment proportionally smaller, and minor prolongation larger.

Measurements (in mm) of 5 large workers from 5 colonies: length of head 2.70-3.00; maximum width of head 3.35-3.60; length of fontanelle 0.27-0.37; width of pronotum 2.10-2.40; width of metanotum 2.15-2.50; length of hind tibia 4.00-4.75.

Comparisons. The imago of *S. obtusus* can be distinguished by its large size and very large eyes; the most similar imagoes are those of *S. grandis* and *S. magnoculus*. The most similar soldier is that of *S. wheeleri*, which has larger marginal teeth located more distally on both mandibles.

Distribution and Geographical Variation. Northern Argentina, Paraguay, southwestern Brazil, and also one record from southern Bolivia and two isolated records from southeastern Brazil (Fig. 325). Soldiers from the vicinities of Cuiabá, Brazil (type locality of *S. silvestrii*) have a more elongate head with sides converging towards front, larger thoracic spines, and more prominent frontal tube.

Biology. *S. obtusus* lives in savannas and grasslands. According to Silvestri (1903: 116), the nest is completely subterranean, but he was able to find only galleries and storage chambers with grasses. He also mentions that only the large workers collect grasses on the surface.



Figs. 225-230. *Syntermes obtusus*. Lectotype imago: 225. head, dorsal view; 226. head, lateral view; 227. pronotum. Large worker: 228. head, dorsal view; 229. head, lateral view; 230. thorax.

Remarks. *S. obtusus* was first described from the imago, and *S. silvestrii* from the soldier. The synonymy of those species was based on a series in Silvestri's collection with soldiers and a queen from the same colony, which was determined both by Silvestri and Emerson as *S. obtusus*. I was not able to examine the queen from that series, but I did examine some soldiers, which are not identical to the type of *S. silvestrii*. There are some intermediate forms, and they may be extremes of a continuum of variation, but the material available is still limited. Therefore, this synonymy should be treated with a certain amount of caution and there is some possibility that there are two species involved.

Syntermes parallelus Silvestri

Syntermes parallelus Silvestri 1923: 318, pl. XV: figs. 1-10 [imago, soldier, worker]; Emerson 1945: 466 [redescription]. Lectotype soldier, here designated: GUYANA. Cattle Trail Survey, Canister Falls, coll. A.A. Abraham, vi.1920 [AMNH]. Paralectotype: one worker, same data as lectotype [AMNH]. No other syntype found in LEFS, except for a slide with a pair of wings.

Syntermes colombianus Snyder 1924: 29, pl. 4: fig 24 [soldier]. Holotype sol-

dier: COLOMBIA. Coll. Winthem, one pinned soldier [MCZ]. Synonymized by Emerson (1945).

Syntermes calvus. Mill 1984a: 406, misidentification, and 1984b: 131 [biology].

Material examined. BRAZIL. *Roraima*. Ilha de Maracá, coll. C.F. Sena, 4.ii.88, one soldier [INPA-393]; coll. A.G. Bandeira, 23.ii.88, soldiers, workers [INPA-672]; coll. F. Luizão, iii.88, one soldier, workers [INPA-748]; coll. A.E. Mill, 09.v.81, soldiers, workers [MPEG-1327]; coll. A.E. Mill, 06.vi.81, one soldier, workers [MPEG-1335]. GUYANA. Kartabo, coll. A.E. Emerson, 2.vi.24, one alate [AMNH]. Oronoque River, coll. N. Weber, 21.vii.36, one soldier [AMNH]. Rupununi Savannahs, coll. J.G. Myers, 1932, one soldier, workers [USNM]. VENEZUELA. Coll. Chaper, 1885, one pinned soldier [MNHN]. *Sucre*. El Rincón, coll. E.M. Cancello, 01.xi.86, soldiers, workers [MZSP-9596, MZSP-9598 and MZSP-9599].

Imago (Figs. 236-238). Eyes small, less than 1/4 width of head; ocelli large; fontanelle small and rounded. Antenna with 19 articles. Anterior corners of pronotum angular, with sharp points; anterior half of lateral margins of pronotum straight and nearly parallel. Wings short, distal part of media and cubitus conspicuous. Head capsule with a few scattered short hairs; postclypeus with two short hairs on anterior margin; pronotum with many hairs on outer margin; tergites with a line of hairs on posterior margin. Head, pronotum and tergites chestnut-brown; sternites brownish yellow; wings brown.

Measurements (in mm) of 2 imagoes from 2 colonies: length of head 2.15-2.25; width of head without eyes 2.55-2.60; length of fontanelle 0.25-0.29; length of pronotum 1.60-1.75; width of pronotum 2.75-3.05; length of hind tibia 4.85-5.10; maximum diameter of eye 0.55-0.59; length of ocellus 0.29-0.29; length of forewing 20.00-21.50; width of forewing 5.50-5.70. Ratios: diameter of eye to width of head 0.22-0.23; length of ocellus to width of head 0.11-0.11; length of fontanelle to width of head 0.10-0.11; width of pronotum to width of head 1.08-1.17; length of wing to width of head 7.84-8.27; length of hind tibia to width of head 1.90-1.96.

Soldier (Figs. 231-235). Head capsule elongate with parallel sides; posterior margin of head rounded; frontal tube prominent, pore not visible in dorsal view. Labrum short, length about equal to width; lateral corners about equal to or a little more than a right angle; median lobe of labrum relatively large. Antenna with 19 articles. Postmentum not constricted, sides of posterior part nearly parallel. Mandibles elongate and straight, except for slightly hooked tip; first marginal tooth of left mandible near the base and small, not extending beyond apical cutting edge; first marginal tooth of right mandible very small and close to the base; apical cutting edge of left mandible evenly curved, except for notch anterior to M1; apical cutting edge of right mandible straight, except for curved tip. Anterior margin of pronotum slightly emarginate; posterior margin nearly straight; thoracic spines weakly developed and slightly upturned; lateral corners of pronotum sharp but not forming conical spines. Head capsule with scattered short bristles, more numerous laterally; base of mandibles without hairs; postmentum with two straight, very short bristles on anterior corners plus many scattered ones; pronotum with many bristles on anterior lobe and margins; meso- and metanotum with numerous bristles on posterior margin and a few on spines and lateral margins; tergites with numerous bristles on posterior half. Head and thorax pale yellow-brown; tergites and sternites yellowish, semi-transparent.

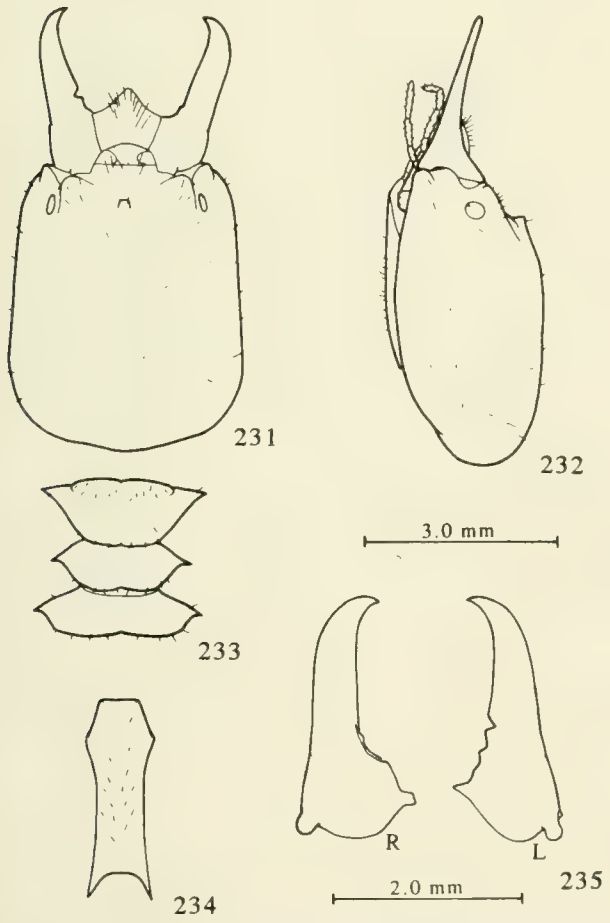
Measurements (in mm) of 5 soldiers from 5 colonies: length of head 4.00-4.90; maximum width of head 2.95-3.65; height of head excluding postmentum 1.95-2.50; length of frontal tube 0.20-0.27; length of left mandible 2.10-2.40; curvature of left mandible 0.35-0.65; distance from M1 to M2 on left mandible 0.20-0.32; width of left mandible 0.54-0.64; length of left M1 0.07-0.10; minimum width of postmentum 0.62-0.76; width of pronotum 2.20-2.60; width of metanotum 2.20-2.60; length of hind tibia 3.10-3.55. Ratio length of head to maximum width of head 1.26-1.37; length of left mandible to length of head 0.49-0.55; length of hind tibia to length of head 0.71-0.78; width of pronotum to maximum width of head 0.70-0.76; distance M1-M2 to length of left mandible 0.10-0.13; height of head to maximum width of head 0.64-0.68; width to length of left mandible 0.25-0.27.

Large worker (Figs. 239-241). Head capsule with a few scattered bristles; postclypeus with 4 bristles. Fontanelle rounded and small. Antenna with 19 articles. Thoracic spines weakly developed. Mandibles similar to those of *S. longiceps*, with narrow molar plate. Gut also similar to that of *S. longiceps*, but material was poorly preserved.

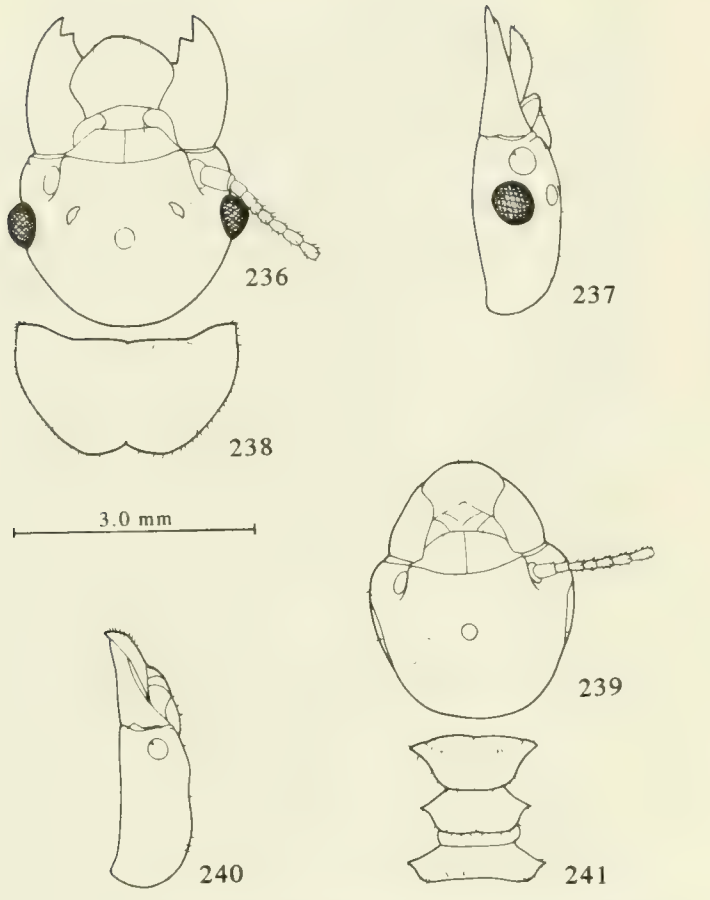
Measurements (in mm) of 5 large workers from 5 colonies: length of head 2.05-2.25; maximum width of head 2.50-2.80; length of fontanelle 0.15-0.22; width of pronotum 1.60-1.70; width of metanotum 1.65-1.90; length of hind tibia 2.90-3.20.

Comparisons. See comparisons under *S. longiceps*.

Distribution and Geographical Variation. Northern Amazonia, including Colombia, Venezuela, Guyana and northern portion of Roraima, Brazil (Fig. 324). Soldiers show some size variation, and specimens from Roraima are a little smaller than average but otherwise there is no evident geographic pattern.



Figs. 231-235. *Syntermes parallelus*, soldier. 231. head, dorsal view; 232. head, lateral view; 233. thorax, dorsal view; 234. postmentum; 235. mandibles, ventral view.



Figs. 236-241. *Syntermes parallelus*. Imago: 236. head, dorsal view; 237. head, lateral view; 238. pronotum. Large worker: 239. head, dorsal view; 240. head, lateral view; 241. thorax.

Biology. *S. parallelus* is a rainforest species. The nest is probably completely subterranean.

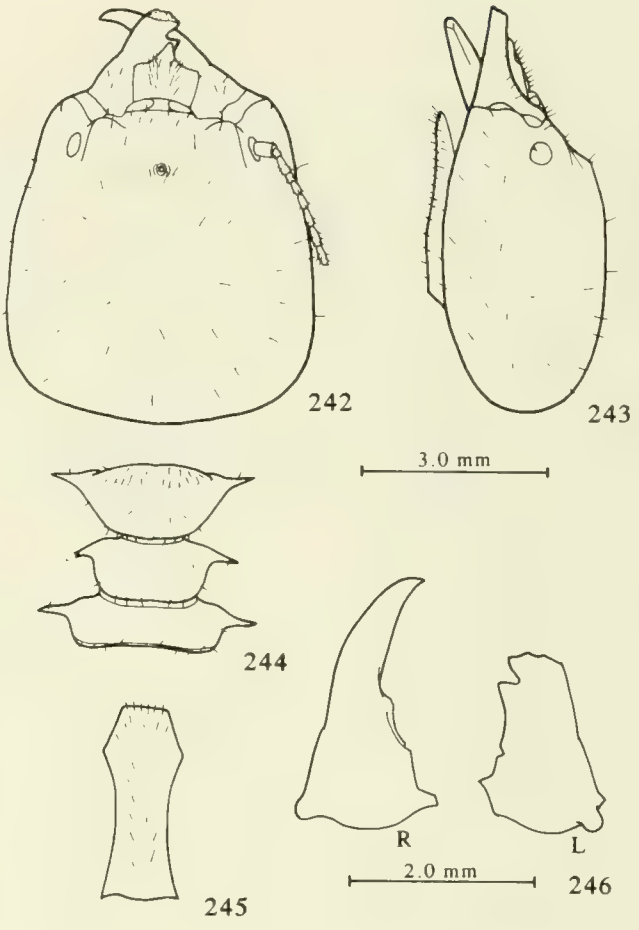
Syntermes peruanus Holmgren

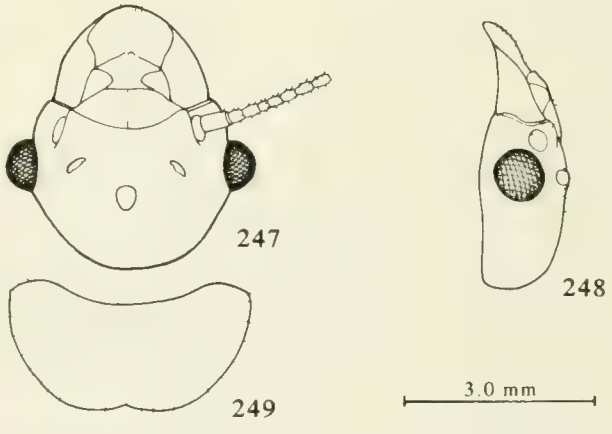
Termes dirus. Holmgren 1906, 545, misidentification [imago, soldier, worker].

Syntermes peruanus Holmgren 1911: 548 [imago, soldier, in key]. Lectotype soldier, here designated: BOLIVIA. *La Paz*, Mojos, coll. N. Holmgren, with broken mandibles [AMNH]. Paralectotypes: two workers in poor condition and 6 whitish alates, also in poor condition [AMNH]. Although the species name refers to Peru, no material from that country was found in Holmgren's collection in NHRS, and part of the type material seems to have been lost. However, Mojos is very close to the Peruvian border and to Holmgren's collection sites in Peru (Fig. 325).

Imago (Figs. 247-249). Eyes moderately large, more than 1/4 width of head; ocelli small; fontanelle roughly triangular and elongate. Antenna with 20 articles. Anterior corners of pronotum moderately angular. Head capsule with many long hairs (but most hairs lost in paratype alates); pronotum with many hairs on outer margin and surface; tergites with many hairs from middle to posterior margin. Specimens incompletely sclerotized.

Measurements (in mm) of one alate: length of head to base of mandibles 2.6; width of head 2.9; length of fontanelle 0.37; length





Figs. 242-246. *Syntermes peruanus*, lectotype soldier. 242. head, dorsal view; 243. head, lateral view; 244. thorax, dorsal view; 245. postmentum; 246. mandibles, ventral view. Left mandible broken.

Figs. 247-249. *Syntermes peruanus*, imago: 247. head, dorsal view; 248. head, lateral view; 249. pronotum. Specimen was incompletely sclerotized; missing hairs.

of pronotum 1.9; width of pronotum 3.65; length of hind tibia 6.0; maximum diameter of eye 0.84; length of ocellus 0.3.

Soldier (Figs. 242-246). Head capsule short, length and width of head about equal; sides slightly converging anteriorly; posterior margin of head rounded or weakly three-lobed; frontal tube very short, pore clearly visible in dorsal view; labrum short, length about equal to width; lateral corners of labrum about equal to a right angle; median lobe of labrum short. Antenna with 19 to 20 articles. Postmentum constricted near the middle. Mandibles curved and moderately elongate; tip of mandibles slightly hooked; first marginal tooth of left mandible small, not extending much beyond apical cutting edge; first marginal tooth of right mandible vestigial; apical cutting edge of left mandible conspicuously sigmoid, forming a notch anterior to M1; apical cutting edge of right mandible straight, except for curved tip. Anterior margin of pronotum slightly emarginate; posterior margin of pronotum nearly straight; lateral projections of pronotum strongly upturned; thoracic spines moderately developed and strongly upturned; pronotum with distinct conical spines; head capsule in dorsal view with many short, straight bristles, more numerous laterally; base of mandibles with a few short hairs; postmentum with numerous short, straight bristles; pronotum with many bristles on anterior lobe and margins, and a few on posterior surface; meso- and metanotum with numerous bristles on posterior margin and a few on spines and lateral margins; tergites with numerous bristles on posterior half.

Measurements (in mm) of the lectotype soldier: length of head 5.10; maximum width of head 5.00; height of head excluding postmentum 2.70; length of frontal tube 0.12; distance from M1 to M2 on left mandible 0.59; width of left mandible 0.77; length of left M1 0.22; minimum width of postmentum 0.86; width of pronotum 3.30; width of metanotum 3.40; length of hind tibia 4.80. Ratio length of head to maximum width of head 1.02; length of hind tibia to length of head 0.94; width of pronotum to maximum width of head 0.66; height of head to maximum width of head 0.54.

Large worker. Because the material available is in very poor condition (just fragments), no description is presented here.

Comparisons. Given the extremely limited material available for study, it is difficult to present a good diagnosis for this species. The imago seems similar to that of *S. wheeleri*, but smaller. The soldier of *S. bolivianus* is smaller, with proportionally smaller marginal teeth on the mandibles, and the sides of the head more parallel. Soldiers of *S. wheeleri* and *S. obtusus* are larger, with shorter thoracic spines.

Distribution. Holmgren (1906) records this species (misidentified as *T. dirus*) from four localities in a small area in southern Peru and northern Bolivia (Fig. 325).

Biology. According to Holmgren (1906: 661), *S. peruanus* (as *T. dirus*) lives in dry areas with open vegetation, and builds a conspicuous epigeal nest (see section on nests above).

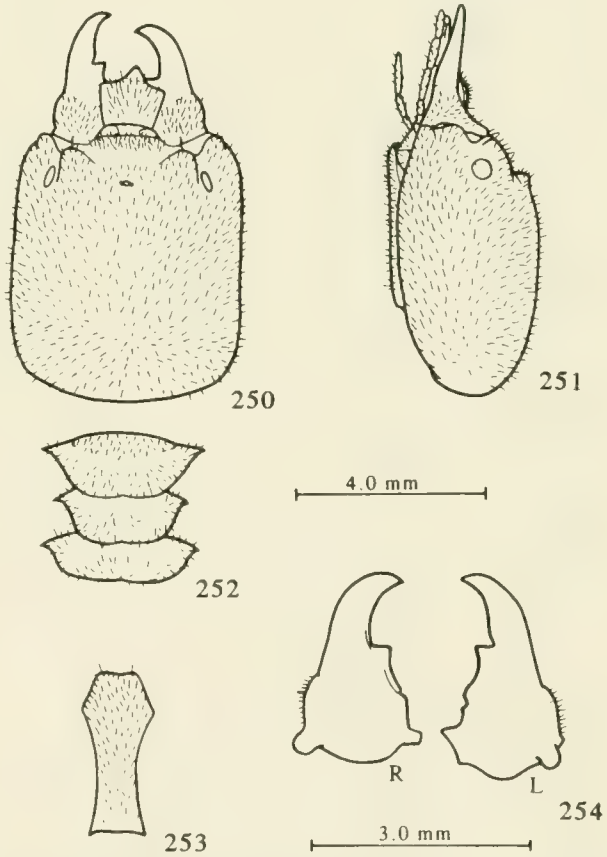
Remarks. The type material of *S. peruanus* was first identified by Holmgren (1906) as *Termes dirus*, as indicated by Holmgren (1911). Unfortunately most specimens from that series seem to have been lost.

Syntermes praecellens Silvestri

Syntermes praecellens Silvestri 1946: 2, fig. 1: 1-14 [imago, soldier, workers]; 6 [biology, nest]. Lectotype soldier, here designated: BRAZIL, *São Paulo*, São Paulo, coll. F. Silvestri, ii.1937 [LEFS]. Silvestri's label: "Brasile: Jabaquara (S. Paolo) Febbraio 1937". Paralectotypes: 5 soldiers, workers, same data as lectotype [LEFS]. Four imagoes, also from S. Paulo, no date, "cotypi! Brasile: S. Paolo: Ypiranga" [LEFS]. One soldier, one nymph, workers, same data as lectotype [AMNH].

Material examined. BRAZIL. *Distrito Federal*. Brasília, coll. H.R. Coles, 27.i.77, soldiers [MZSP-9297]. *Minas Gerais*. Passa Quatro, coll. E. R. Wagner, one soldier, one worker [ISNB]. Rio Preto, coll. C.R. Goncalves, 08.i.68, soldiers, workers [MZSP-371]; coll. C.R. Goncalves, 08.i.68, soldiers, alates [MZSP-1866]. *Paraná*. Lapa, coll. C.R. Goncalves, 20.x.54, soldiers, workers [MZSP-4664]. *Santa Catarina*. Nova Teutonia, coll. F. Plaumann, ii.60, one soldier [MZSP-1853]. *São Paulo*. Atibaia, coll. R.L. Araujo, 19.iii.46, soldiers, workers [MZSP-2929]. Ibiuna, coll. U. Kawazoe, 08.iii.70, soldiers [MZSP-4759]. S.J. dos Campos, coll. D.L. Tiemann, 26.x.69, soldiers, workers [MZSP-4743]. Santo Andre, coll. L. Stowbnenko, ii.62, soldiers, workers [MZSP-1858]. São Paulo, coll. Silvestri, 07.ix.37, soldiers, workers [MZSP-1835]; coll. L.C. Almeida, 17.viii.60, soldiers, workers [MZSP-1848]; coll. Silvestri, 09.x.37, alates [MZSP-2945]; coll. E. Rabello, soldiers, workers [MZSP-3827]; coll. R.L. Araujo, 05.iii.74, one soldier, workers [MZSP-5347]; coll. R.L. Araujo, 29.ix.70, alates [MZSP-5393]; coll. R.L. Araujo, 28.ii.75, soldiers, workers [MZSP-5898]; coll. L.R. Fontes, 03.i.79, soldiers, workers [MZSP-7727]; coll. C.R.F. Brandão, 21.ii.83, soldiers, workers [MZSP-8385]; coll. E.M. Cancello, 27.xi.86, alates [MZSP-8997]; coll. E.P. Teixeira, 29.xi.87, soldiers, workers [MZSP-9757].

Imago (Figs. 255-257). Eyes small, less than 1/4 width of head; ocelli small; fontanelle nearly triangular and small. Antenna with



Figs. 250-254. *Syntermes praecellens*, soldier. 250. head, dorsal view; 251. head, lateral view; 252. thorax, dorsal view; 253. postmentum; 254. mandibles, ventral view.

20 articles. Anterior corners of pronotum moderately angular. Wings very long (Fig. 9); distal part of media and cubitus inconspicuous. Head capsule with numerous straight bristles; postclypeus with about 14 bristles; pronotum with many hairs on outer margin and surface; tergites with many hairs from middle to posterior margin. Head dark brown; pronotum light chestnut, contrasting with head; tergites chestnut-brown; sternites light chestnut and chestnut-brown, darker near lateral margins; wings hyaline, except for brownish proximal and costal areas.

Measurements (in mm) of 4 imagoes from 3 colonies: length of head 2.75-2.90; width of head without eyes 3.20-3.40; length of fontanelle 0.20-0.30; length of pronotum 1.95-2.10; width of pronotum 3.65-3.75; length of hind tibia 5.20-6.20; maximum diameter of eye 0.74-0.82; length of ocellus 0.27-0.32; length of forewing 36.00-36.50; width of forewing 8.40-8.50. Ratios: diameter of eye to width of head 0.22-0.24; length of ocellus to width of head 0.08-0.10; length of fontanelle to width of head 0.06-0.09; width of pronotum to width of head 1.07-1.17; length of wing to width of head 10.75-10.90; length of hind tibia to width of head 1.53-1.85.

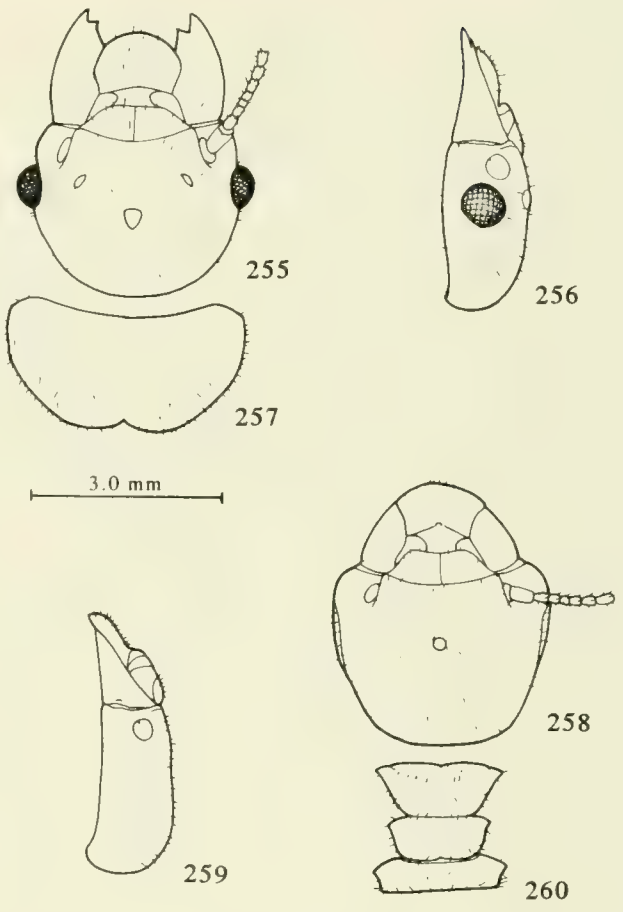
Soldier (Figs 250-254). Head capsule elongate with sides parallel; posterior margin of head rounded; frontal tube prominent, pore not visible in dorsal view; labrum short, length about equal to width; lateral corners of labrum about equal to a right angle; median lobe of labrum short. Antenna with 19 articles. Postmentum slightly constricted in the middle. Mandibles short and robust, with inflated bases; tip of mandibles slightly hooked; first marginal tooth of left mandible near the middle and large, extending well beyond apical cutting edge; first marginal tooth of right mandible large; angle between right M1 and apical cutting edge a little more than 90°; apical cutting edge of left mandible sigmoid but not forming a notch anterior to M1; apical cutting edge of right mandible evenly curved. Anterior margin of pronotum nearly rounded to slightly emarginate; posterior margin nearly straight; thoracic spines weakly developed and not upturned; lateral corners of pronotum sharp but not forming conical spines; head capsule and postmentum densely covered with very short, straight bristles; postclypeus densely covered with short hairs; base of mandibles with numerous short hairs; pronotum with many short bristles on entire surface, more numerous on anterior lobe; mesonotum, metanotum and tergites densely covered with short, straight bristles.

Measurements (in mm) of 6 soldiers from 6 colonies: length of head 5.40-5.80; maximum width of head 4.60-5.00; height of head excluding postmentum 2.90-3.10; length of frontal tube 0.22-0.27; length of left mandible 2.30-2.50; curvature of left mandible 0.65-0.80; distance from M1 to M2 on left mandible 0.45-0.67; width of left mandible 0.77-0.87; length of left M1 0.13-0.20; minimum width of postmentum 0.76-0.87; width of pronotum 2.90-3.20; width of metanotum 2.80-3.30; length of hind tibia 4.60-5.30. Ratio length of head to maximum width of head 1.10-1.21; length of left mandible to length of head 0.41-0.45; length of hind tibia to length of head 0.82-0.98; width of pronotum to maximum width of head 0.63-0.67; distance M1-M2 to length of left mandible 0.20-0.28; height of head to maximum width of head 0.61-0.65; width to length of left mandible 0.33-0.35.

First form soldier. Described by Silvestri (1946: 5, Fig. I, 6-9). No material examined. Smaller than normal soldier, with fewer hairs on head and more slender mandibles.

Large worker (Figs. 258-260). Head capsule and postclypeus densely covered with short bristles. Fontanelle small and rounded. Antenna with 20 articles. Thoracic spines weakly developed. Mandibles similar to those of *S. dirus*, with narrow molar plate and basal notch forming an obtuse angle. Gut very similar to that of *S. barbatus*; major midgut prolongation of mixed segment a little more elongate; minor prolongation identical.

Measurements (in mm) of 5 large workers from 5 colonies: length of head 2.50-2.75; maximum width of head 3.10-3.30; length of fontanelle 0.24-0.25; width of pronotum 1.80-1.90; width of metanotum 1.90-2.10; length of hind tibia 3.80-4.05.



Figs. 255-260. *Syntermes praecellens*. Imago: 255. head, dorsal view; 256. head, lateral view; 257. pronotum. Large worker: 258. head, dorsal view; 259. head, lateral view; 260. thorax.

Comparisons. The imago of *S. praecellens* is not particularly similar to the imago of any other species of *Syntermes* and can be identified by its very long and hyaline wings, small triangular fontanelle, numerous bristles on top of head, relatively small eyes, and dark brown head contrasting with chestnut pronotum. The soldier is very distinct with its elongate head densely covered with short bristles, short and robust mandibles, and weakly developed thoracic spines. The most similar soldier is that of *S. territus*, which has a less elongate head with fewer bristles and smaller mandibular teeth.

Distribution and Geographical Variation. Except for the isolated record from Brasília, all samples come from a narrow band along the coastal mountain range of southern Brazil (Fig. 320). Apparently this species is associated with a particular kind of habitat that occurs on mountain slopes. Unfortunately, most samples come from urban areas and it is difficult to determine which habitat was there prior to urbanization. Most likely it was a kind of grassland that occurs at some elevation. There is little morphological variation between most areas, but soldiers from Minas Gerais have less numerous hairs on the head. The single sample from Brasília has

somewhat different soldiers, with less numerous hairs on the head, and slightly longer mandibles.

Biology. The nest (Fig. 4) is subterranean (see section about nests for more information), but some label notes indicate that sometimes there are small piles of soil on the surface. All samples were collected in grassland areas.

Syntermes spinosus (Latreille)

Termes spinosum Latreille 1804: 62 [soldier]. Holotype soldier: "Afrique (?)", unknown locality, probably French Guyana, labelled by A.E. Emerson as the holotype of *S. spinosus* based on a statement by J. Desneux; pinned and in poor condition [ISNB]. No paratypes known.

Syntermes spinosus, Araujo 1977: 54 [catalog].

Termes costatus Rambur 1842: 305 [imago]. Holotype imago: FRENCH GUIANA: Cayenne, coll. Serville. [ISNB], not examined. Synonymyzed by Emerson in Araujo (1977: 54).

Termes decumanus Erichson 1848: 582 [soldier only]. Lectotype soldier, here designated: GUYANA, coll. Schomburgk [ZMHU]. Alates of the same series are *S. grandis*.

Syntermes snyderi Emerson 1925: 358, fig. 44 [imago, soldier]; Emerson 1945: 446 [redescription]. Holotype soldier: GUYANA. Kartabo, coll. A.E. Emerson, 1919 [AMNH]. Synonymized by Emerson in Araujo (1977: 54).

Syntermes solidus Emerson 1945: 447, fig. 6 [soldier]. Holotype soldier: FRENCH GUIANA, St. Jean, Moroni R., coll. Le Moult [AMNH].

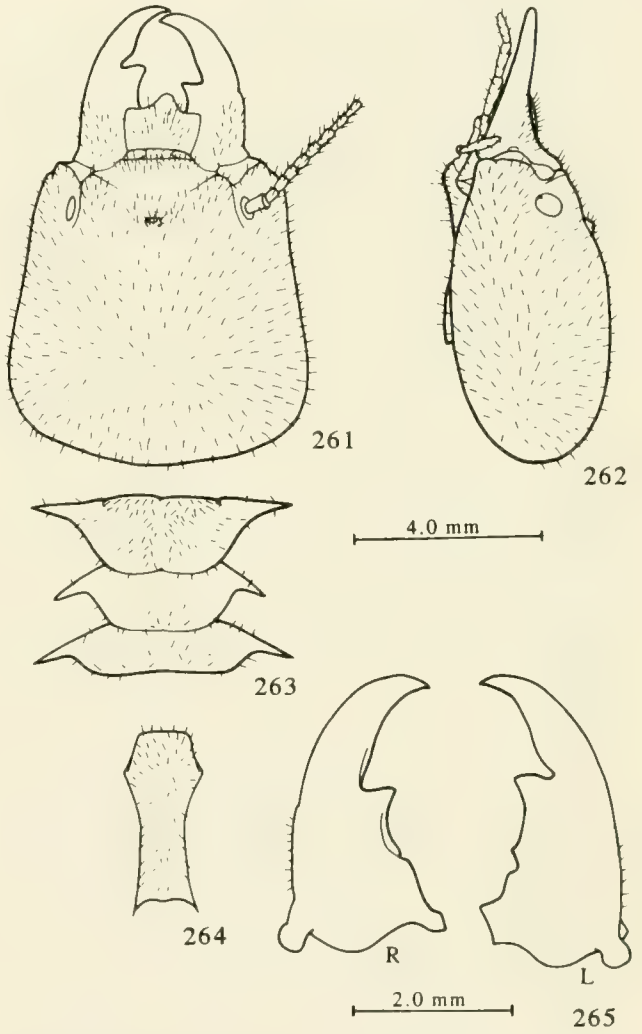
Syntermes chaquimayensis parvinasus Emerson 1945: 450, fig. 7 [soldier]. Holotype soldier: COLOMBIA. *Vaupés*. Rio Uaupés, 1906 [AMNH].

Syntermes robustus Constantino 1991: 221, fig. 31-34 [imago, soldier]. Holotype soldier: BRAZIL. *Amazonas*. Maraã, coll. R. Constantino, 17.x.1988 [MPEG-2885].

Syntermes lighti, Mill 1984b: 132, misidentification [biology].

Material examined. BRAZIL. *Amazonas*. Manaus, coll. R.S. Bradley, 18.ix.78, one soldier, workers [MPEG-493]; coll. A.G. Bandeira, 16.viii.76, soldiers, workers [MPEG-2]; coll. T.C. Fletcher, 19.i.1863, alates [MCZ]; coll. O.F. Souza, 21.v.86, soldiers, workers [MEUV]; coll. O.F. Souza, soldiers, one worker [MEUV]. Manaus: Reserva Ducke, coll. R.I. Barbosa, 7.vi.92, soldiers, workers [INPA-1]. Maranhoto: Rio Jau, coll. H.O. Schubart, 06.iv.77, soldiers, workers [MPEG-74]. Porto Urucu: Rio Urucu, coll. T.C.S. Pires, 22.xi.89, soldiers, workers [MPEG-3297]; coll. T.C.S. Pires, 26.xi.89, soldiers, workers [MPEG-3299]; coll. T.C.S. Pires, 19.xi.89, soldiers, workers [MPEG-3308 and MPEG-3309]. *Mato Grosso*. Chapada dos Parecis, coll. E.Z.F. Setz, 24.i.80, soldiers [MZSP-8766]. Iquê-Juruena, coll. A.E. Mill, 04.viii.80, one soldier, workers [MPEG-1302]; coll. A.E. Mill, 10.viii.80, soldiers, one worker [MZSP-8401]. Xavantina, coll. A.G.A. Mathews, iv.68, soldiers, workers [BMNH]; coll. A.G.A.Mathews, 8.xii.67, alates [BMNH]. *Pará*. Monte Dourado, coll. W.L. Overal, 02.xi.79, one soldier, workers [MPEG-3896]. Serra dos Carajás, 26.x.83, soldiers, workers [MPEG-3897]; coll. M.F. Torres, 16.iv.83, one soldier [MPEG-1528]; coll. A.G. Bandeira, 13.ix.83, soldiers, one worker [MPEG-1604]; coll. R. Moraes, 11.vi.85, soldiers [MPEG-2372]. Tucuruí: Chiqueirinho, coll. M.F. Torres, 06.iv.84, soldiers, workers [MPEG-2131]. *Roraima*. Ilha de Maracá, coll. A.G. Bandeira, 19.ii.88, soldiers, workers [MZSP-9120]; coll. A.G. Bandeira, 23.x.87, soldiers, workers [INPA-212 and 326]; coll. A.G. Bandeira, 11.ii.88, one soldier, workers [INPA-455]; coll. A.G. Bandeira, 12.ii.88, soldiers, workers [INPA-497, 499 and 511]; coll. C.F. Sena, 17.ii.88, soldiers, workers [INPA-619]; coll. A.G. Bandeira, 19.ii.88, soldiers, workers [INPA-669]. Ireng River, viii.11, soldiers [AMNH]. COLOMBIA. *Vaupés*. Yebaka, coll. S.H. Jones, soldiers, alates [BMNH]. Rio Uaupés, 1906, two soldiers, paratypes of *S. chaquimayensis parvinasus* [AMNH]; two other vials with many soldiers, same data but not labelled as paratypes [AMNH]. Yapú: Rio Papuri, coll. D. Dufour, 12.vi.77, soldiers [USNM]; coll. D. Dufour, 27.iv.77, soldiers, one worker [USNM]; coll. D. Dufour, 27.iii.77, soldiers [USNM]. FRENCH GUIANA. Coll. Desutter & Gran, 1.vii.88, one soldier [MNHN]. Cayenne, one soldier [ISNB]. Oiapoque, coll. J. Gray, 1900, one soldier [MNHN]. GUYANA. Coll. R. Schomburgk, one soldier [BMNH]. Bartica District, coll. A.E. Emerson, 1919, one soldier, one alate [AMNH]. Demerara, coll. Bowerbank, one soldier [BMNH]. SURINAME. Jodensavanne, coll. M.A. Knoppe, vi.57, soldiers, workers [MZSP-9765]. Oelemarie, coll. Raatzerer, 1938, soldiers [AMNH]. VENEZUELA. Sarare, coll. F. Gray, 1893, one soldier [ISNB]; coll. J. Gray, 1895, one soldier [MNHN].

Imago (Figs. 274-276). Eyes small, less than 1/4 width of head; ocelli small; fontanelle rounded and moderately large. Antenna with 20 articles. Anterior corners of pronotum angular, with sharp points; lateral margins of pronotum slightly sigmoid, with anterior half nearly parallel. Wings short, distal part of media and cubitus conspicuous. Head capsule with a few scattered bristles; postclypeus with 6-8 bristles; pronotum with many hairs on outer margin and a few scattered ones on surface; tergites with many hairs near posterior margin and scattered very short hairs on posterior half. Head and pronotum light chestnut; tergites chestnut-brown; sternites light chestnut; wings brown to dark brown.



Figs. 261-265. *Syntermes spinosus*, soldier from central Amazonia. 261. head, dorsal view; 262. head, lateral view; 263. thorax, dorsal view; 264. postmentum; 265. mandibles, ventral view.

Measurements (in mm) of 7 imagoes from 5 colonies: length of head 2.65-3.05; width of head without eyes 3.00-3.40; length of fontanelle 0.37-0.54; length of pronotum 2.00-2.40; width of pronotum 3.70-4.55; length of hind tibia 6.40-7.10; maximum diameter of eye 0.67-0.72; length of ocellus 0.29-0.35; length of forewing 26.00-30.00; width of forewing 6.60-7.70. Ratios: diameter of eye to width of head 0.20-0.24; length of ocellus to width of head 0.09-0.10; length of fontanelle to width of head 0.11-0.16; width of pronotum to width of head 1.23-1.36; length of wing to width of head 8.51-9.03; length of hind tibia to width of head 1.97-2.20.

Soldier (Figs. 261-270). Head capsule short to moderately elongate, sides converging towards front; posterior margin of head rounded; frontal tube prominent, or short, in a small depression, pore usually not visible in dorsal view. Labrum short, length about equal to width; lateral corners of labrum about equal to a right angle; median lobe of labrum short. Antenna with 19 or 20 articles. Postmentum not constricted, sides of posterior part nearly parallel. Mandibles curved and moderately elongate; tip slightly hooked; first marginal tooth of left mandible large, extending well beyond apical cutting edge; first marginal tooth of right mandible large; angle between right M1 and apical cutting edge less than 90°; apical cutting edge of left mandible sigmoid; apical cutting edge of right mandible slightly sigmoid or straight, except for curved tip. Anterior margin of pronotum slightly emarginate; posterior margin slightly emarginate; thoracic spines well-developed and strongly upturned; pronotum with distinct, large conical spines. Head capsule densely covered with short, straight bristles; clypeal region densely covered with short hairs; base of mandibles with numerous short hairs; postmentum densely covered with short, straight bristles; pronotum with many bristles on entire surface, more numerous on anterior lobe; meso- and metanotum with numerous hairs near hind and lateral margins and some on spines; tergites with numerous bristles on posterior half.

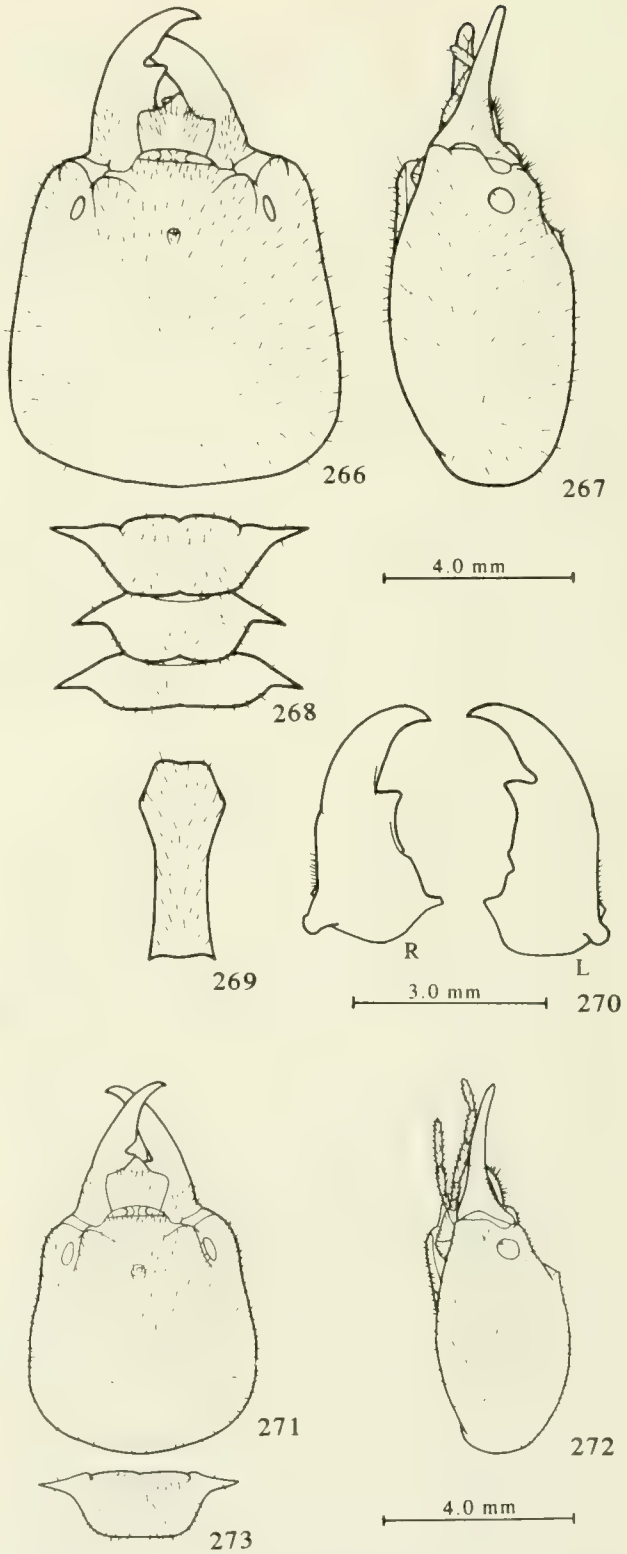
Measurements (in mm) of 22 soldiers from 20 colonies: length of head 5.45-7.20; maximum width of head 5.10-7.60; height of head excluding postmentum 2.90-4.10; length of frontal tube 0.15-0.30; length of left mandible 3.00-3.60; curvature of left mandible 1.00-2.10; distance from M1 to M2 on left mandible 0.66-1.09; width of left mandible 0.87-1.26; length of left M1 0.25-0.55; minimum width of postmentum 0.87-1.13; width of pronotum 4.30-5.70; width of metanotum 4.30-5.70; length of hind tibia 5.80-6.50. Ratio length of head to maximum width of head 0.93-1.11; length of left mandible to length of head 0.46-0.59; length of hind tibia to length of head 0.86-1.12; width of pronotum to maximum width of head 0.70-0.89; distance M1-M2 to length of left mandible 0.21-0.33; height of head to maximum width of head 0.51-0.60; width to length of left mandible 0.27-0.40.

First form soldier (Figs. 271-273). Conspicuously smaller than the normal soldier, and with more elongate mandibles with smaller marginal teeth. Pilosity and thoracic spines similar to those of normal soldier.

Large worker (Figs. 277-279). Head capsule and postclypeus with many straight bristles. Fontanelle rounded and relatively small. Antenna with 20 articles. Thoracic spines well developed. Mandibles (Fig. 19) with relatively narrow molar plate and basal notch of a little more than 90°. Gut similar to that of *S. dirus*, but major midgut prolongation of mixed segment is wider.

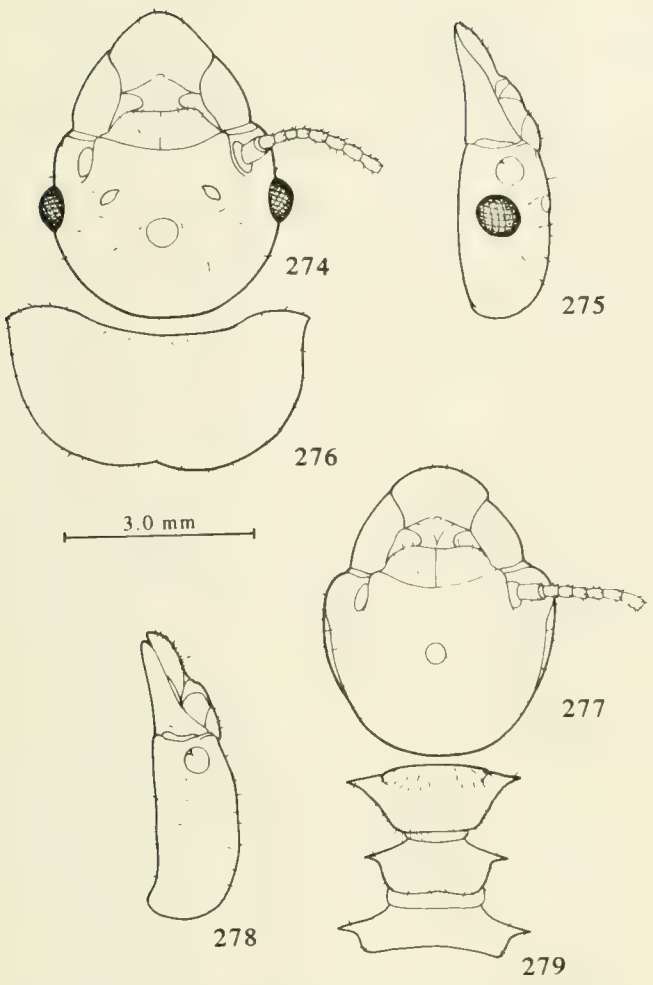
Measurements (in mm) of 13 large workers from 11 colonies: length of head 2.80-3.15; maximum width of head 3.35-3.80; length of fontanelle 0.25-0.34; width of pronotum 2.55-3.10; width of metanotum 2.75-3.40; length of hind tibia 4.45-5.25.

Comparisons. The imago of *S. spinosus* is similar to those of *S. dirus*, *S. cearensis*, *S. aculeosus*, *S. chaquimayensis* and *S. tanygnathus*, and it is difficult to distinguish from some of these species. *S. dirus*, *S. cearensis* and *S. aculeosus* have shorter hairs on the head, and *S. aculeosus* also has a larger fontanelle and different pronotum; *S. tanygnathus* has an antenna with 21 articles; *S. chaquimayensis* has



Figs. 266-270. *Syntermes spinosus*, soldier from western Amazonia, paratype of *S. chaquimayensis parvinasus*. 266. head, dorsal view; 267. head, lateral view; 268. thorax, dorsal view; 269. postmentum; 270. mandibles, ventral view.

Figs. 271-273. *Syntermes spinosus*, first form soldier. 271. head, dorsal view; 272. head, lateral view; 273. pronotum.



Figs. 274-279. *Syntermes spinosus*. Imago from Guyana: 274. head, dorsal view; 275. head, lateral view; 276. pronotum. Large worker: 277. head, dorsal view; 278. head, lateral view; 279. thorax.

longer and more numerous bristles on the head. The soldier is most similar to that of *S. chaquimayensis*, but is usually conspicuously larger, with more elongate mandibles and larger marginal teeth. However, *S. spinosus* shows considerable morphological variation and may be difficult to separate from *S. chaquimayensis*.

Distribution and Geographical Variation. *S. spinosus* occurs in most parts of Amazonia, from Venezuela to Mato Grosso, Brazil, including the Guianas, and there is also one isolated southern record near the Paraná River (Fig. 320). The long list of synonyms is a good indication of how variable this species is. Soldiers from Suriname and French Guiana tend to be larger than elsewhere, with proportionally wider head and thorax, and prominent frontal tube, and some would correspond to Emerson's *S. solidus*. Specimens from Guyana and Venezuela are intermediate, and would closely fit the description of *S. snyderi*. Those from Colombia are also larger than average, with less numerous hairs on the head and a smaller frontal tube located in a small depression, and would correspond to *S. chaquimayensis parvinasus*. Specimens from central Amazonia are a little smaller, with slightly elongate head and short frontal tube, and correspond to *S. robustus*. However, the study of large series indicates that the variation is continuous, and all these forms belong to the same species. Some soldiers from Mato Grosso also have less numerous hairs on the head.

Biology. *S. spinosus* is a forest species which seems to be very common in the Amazon region. Its nest was described by Emerson (1938) and is similar to that of *S. dirus* (see section about nests above).

Remarks. The smaller soldiers were present in a few samples mixed with normal soldiers, and in some cases without the normal soldiers. They are here interpreted as first form soldiers, which appear in young colonies. Although there is no direct evidence that they are from young colonies, the facts that they were collected with normal soldiers of *S. spinosus*, have pilosity and thoracic nota similar to normal soldiers and fit the expected size and morphology of a first form soldier (based on the first form soldier of *S. praecellens*) support this interpretation. Also, there is no evidence of parasitism or disease, which could also cause the appearance of abnormal soldiers. There is, however, a remote possibility that they belong to a different species.

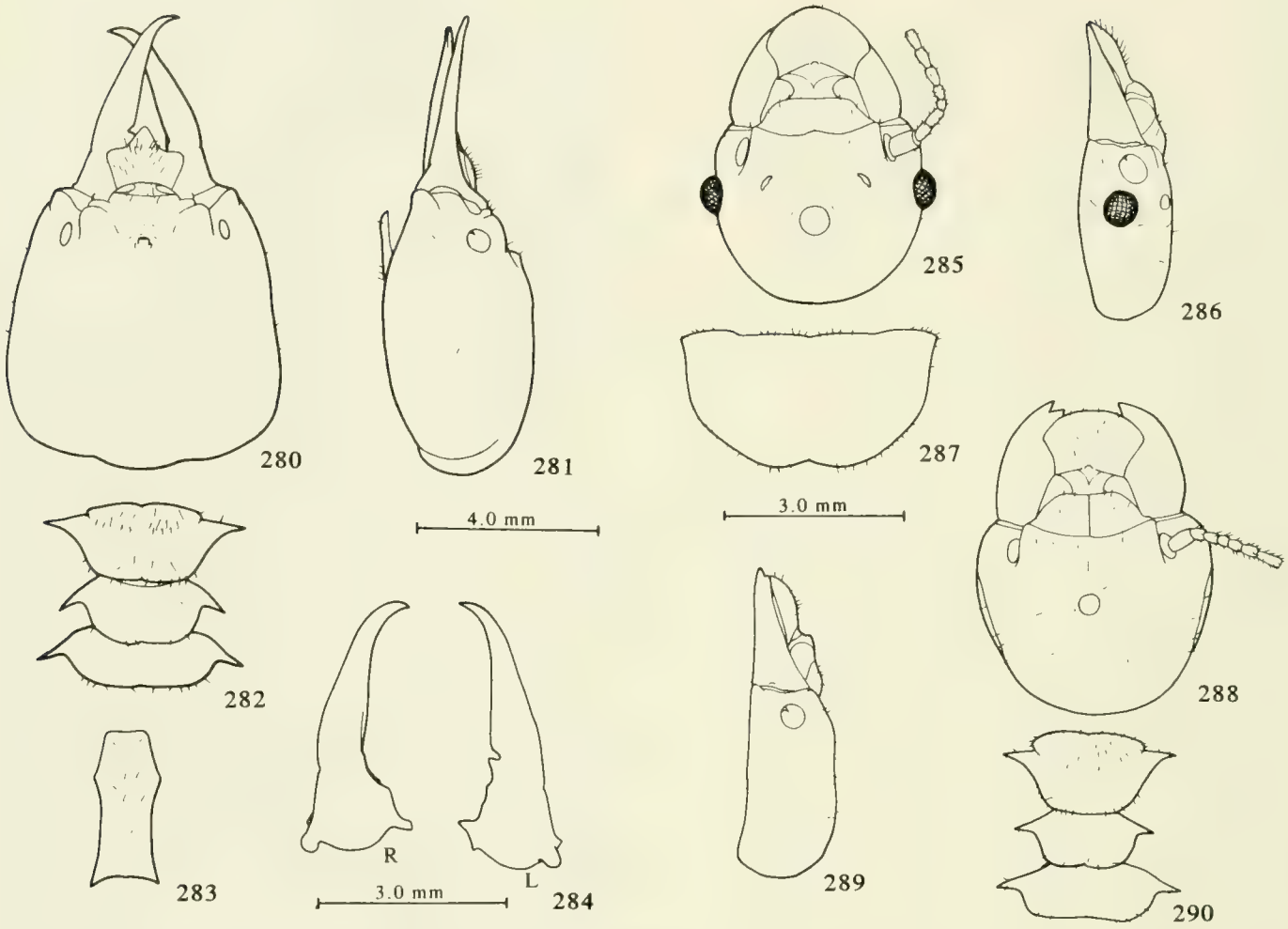
Syntermes tanygnathus, new species

Holotype soldier: BRAZIL. *Amazonas*. Aldeia São João, Rio Tiquié, coll. R.B. Barthem, 01.i.91 [MPEG-3805]. Paratypes. Seven soldiers, same data as holotype [MPEG-3805]. COLOMBIA. Ohea (?), coll. S.H. Jones, soldiers, one worker, alates [BMNH]. *Amazonas*. Chorrera, coll. J. Gashe, four pinned soldiers [MNHN]. *Vaupes*. Yapú, Rio Papuri, coll. D. Dufour, 23.v.77, soldiers, one worker, in two vials [USNM].

Imago (Figs. 285-287). Eyes small, less than 1/4 width of head; ocelli small; fontanelle rounded and moderately large. Antenna with 21 articles. Anterior corners of pronotum angular, with sharp points; lateral margins of pronotum slightly sigmoid. Wings long (Fig. 11); distal part of media and cubitus conspicuous. Head capsule with a few scattered hairs; postclypeus with 6-8 hairs; pronotum with many hairs on outer margin; tergites with many hairs near posterior margin and scattered very short hairs on posterior half. Head and pronotum light chestnut; tergites chestnut-brown; sternites light chestnut; wings brown.

Measurements (in mm) of 2 imagoes from one colony: length of head 2.75-2.95; width of head without eyes 3.30-3.40; length of fontanelle 0.34-0.50; length of pronotum 2.20-2.30; width of pronotum 3.80-4.15; length of hind tibia 6.70-6.90; maximum diameter of eye 0.71-0.72; length of ocellus 0.25-0.30; length of forewing 30.00-32.00; width of forewing 7.60-7.70. Ratios: diameter of eye to width of head 0.21-0.22; length of ocellus to width of head 0.08-0.09; length of fontanelle to width of head 0.10-0.15; width of pronotum to width of head 1.15-1.22; length of wing to width of head 9.09-9.41; length of hind tibia to width of head 2.03-2.03.

Soldier (Figs. 280-284). Head capsule short, length and width of head about equal, sides converging towards front; posterior margin of head conspicuously three-lobed; frontal tube prominent, pore not visible in dorsal view. Labrum short and distinctly three-lobed; lateral corners of labrum forming an acute angle; median lobe of labrum not elongate. Antenna with 20-21 articles. Postmentum relatively short and wide; slightly constricted in the middle. Mandibles slender and elongate; tip of mandibles slightly hooked; first marginal tooth of left mandible near the base and small, not extending much beyond apical cutting edge; first marginal tooth of right mandible vestigial and close to the base; apical cutting edge of left mandible straight except for curved tip and notch anterior to M1; apical cutting edge of right mandible slightly sigmoid. Anterior margin of pronotum slightly emarginate; posterior margin nearly straight; lateral projections of pronotum strongly upturned; thoracic spines well-developed and strongly upturned; pronotum with distinct conical spines. Head capsule with a few scattered, short bristles; postclypeus with only 4 hairs; base



Figs. 280-284. *Syntermes tanygnathus*, sp.n., soldier. 280. head, dorsal view; 281. head, lateral view; 282. thorax, dorsal view; 283. postmentum; 284. mandibles, ventral view.

Figs. 285-290. *Syntermes tanygnathus*, sp.n.. Imago: 285. head, dorsal view; 286. head, lateral view; 287. pronotum. Large worker: 288. head, dorsal view; 289. head, lateral view; 290. thorax.

of mandibles without hairs; postmentum with scattered short, straight bristles; pronotum with many bristles on anterior lobe and posterior margin, plus scattered ones near posterior margin and on spines; meso- and metanotum with numerous bristles on posterior margin and a few on spines and lateral margins; tergites with a few bristles near hind margin.

Measurements (in mm) of 4 soldiers from 4 colonies: length of head 5.90-6.30; maximum width of head 5.70-6.30; height of head excluding postmentum 3.30-3.40; length of frontal tube 0.15-0.22; length of left mandible 3.80-4.10; curvature of left mandible 0.80-1.00; distance from M1 to M2 on left mandible 0.34-0.45; width of left mandible 0.82-0.87; length of left M1 0.15-0.18; minimum width of postmentum 1.02-1.14; width of pronotum 4.30-4.60; width of metanotum 4.50-4.60; length of hind tibia 7.00-7.20. Ratio length of head to maximum width of head 1.00-1.05; length of left mandible to length of head 0.63-0.67; length of hind tibia to length of head 1.14-1.20; width of pronotum to maximum width of head 0.73-0.77; distance M1-M2 to length of left mandible 0.09-0.11; height of head to maximum width of head 0.54-0.58; width to length of left mandible 0.21-0.22.

Large worker (Figs. 288-290). Head capsule large, with scattered straight hairs. Fontanelle rounded and small. Antenna with 20-21 articles. Mandibles similar to those of *S. dirus*, with relatively narrow molar plate and a basal notch of a little more than 90°. Gut (examined in a soldier) similar to *S. dirus*, but mixed segment with relatively larger midgut prolongations; minor prolongation more elongate; mixed segment with a conspicuous protuberance on the opposite side of the insertion of Malpighian tubules (Fig. 35).

Measurements (in mm) of 1 large worker: length of head 3.10; maximum width of head 3.75; length of fontanelle 0.34; width of pronotum 2.80; width of metanotum 2.80; length of hind tibia 5.60.

Comparisons. The alate is very similar to that of *S. spinosus*, which has the antenna with only 20 articles. The soldier is very distinct and can be easily identified by its short head with conspicuously three-lobed posterior margin, very elongate mandibles with reduced marginal teeth, well-developed thoracic spines, and relatively long legs.

Distribution. Apparently limited to a small region of western Amazonia, near the border between Brazil and Colombia (Fig. 319).

The few samples available do not show much variation.

Biology. The limited information available indicates that this is a forest species. One label indicates an "earth pile", and the nest may be similar to that of *S. dirus*.

Remarks. Soldiers of *S. tanygnathus* are consumed by indigenous peoples of the region where this species occurs.

Syntermes territus Emerson

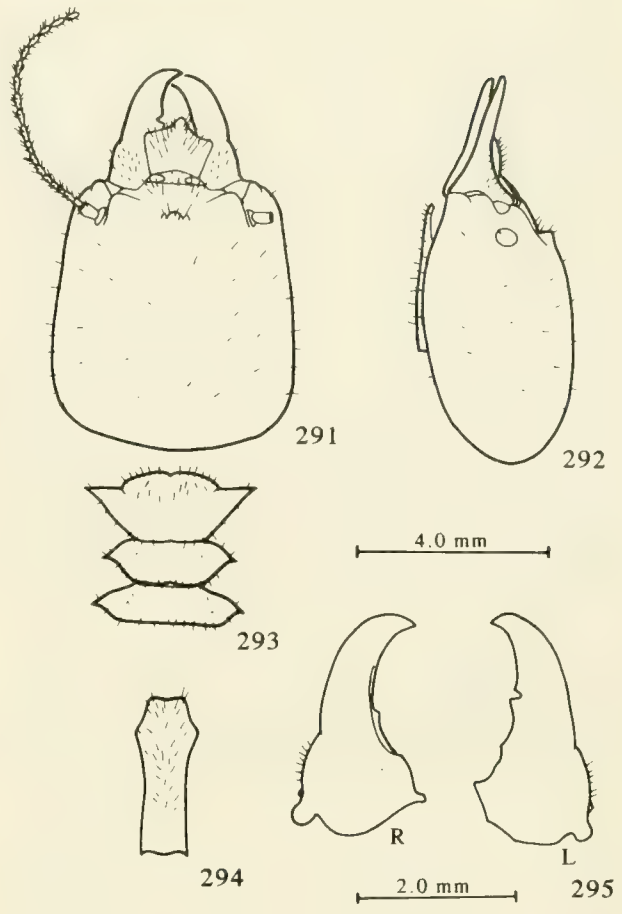
Syntermes territus Emerson 1925: 359, fig. 45 [imago, soldier]; Emerson 1945: 464 [redescription]. Holotype soldier: GUYANA. Kartabo, coll. A.E. Emerson, 1919 [AMNH]. Paratypes: one soldier, 5 alates, one worker, same data as holotype [AMNH].

Material examined. BRAZIL. *Amazonas*. Cururuzinho, R. Autaz, coll. A. Roman, 22.x.14, one soldier, workers [AMNH]. *Ceará*. Guaramiranga, coll. C.R. Gonçalves, 26.xii.48, soldiers, one worker [AMNH]; coll. C.R. Goncalves, 18.i.45, soldiers [MZSP-2927]; coll. C.R. Goncalves, 25.xii.48, soldiers, workers [MZSP-3148]. *Pará*. Serra dos Carajás, coll. R. Moraes, 11.vi.85, one soldier [MPEG-3461]. GUYANA. Bartica District, coll. A.E. Emerson, soldiers, workers [AMNH]. Kamakusa, coll. H. Lang, xi.22, soldiers, workers [BMNH]; coll. H. Lang, xii.1922, soldiers, one worker [AMNH]. Kartabo, coll. A.E. Emerson, 5.iv.24, one soldier, workers, queen, king [AMNH].

Imago (Figs. 296-298). Eyes small, less than 1/4 width of head; ocelli small; fontanelle rounded and relatively small. Antenna with 19 or 20 articles. Anterior corners of pronotum moderately angular. Wings short (Fig. 10), distal part of media and cubitus conspicuous. Head capsule with a few scattered short bristles; postclypeus with two hairs on anterior margin and two near middle; pronotum with many hairs on outer margin and an occasional one on surface; tergites with a line of hairs on posterior margin. Head, pronotum and tergites chestnut-brown; sternites brownish yellow; wings brown.

Measurements (in mm) of 3 imagoes from 2 colonies: length of head 2.15-2.50; width of head without eyes 2.60-2.85; length of fontanelle 0.25-0.30; length of pronotum 1.75-1.90; width of pronotum 3.03-3.25; length of hind tibia 5.00-5.40; maximum diameter of eye 0.59-0.67; length of ocellus 0.25-0.30; length of forewing 25.00; width of forewing 6.50. Ratios: diameter of eye to width of head 0.21-0.24; length of ocellus to width of head 0.10-0.11; length of fontanelle to width of head 0.09-0.12; width of pronotum to width of head 1.07-1.17; length of wing to width of head 8.77; length of hind tibia to width of head 1.75-1.96.

Soldier (Figs. 291-295). Head capsule elongate with nearly parallel sides; posterior margin of head rounded; frontal tube prominent, pore not visible in dorsal view; labrum short, length about equal to width; lateral corners of labrum about equal to a right angle; median lobe of labrum short. Antenna with 19 articles. Postmentum not constricted, sides of posterior part nearly parallel. Mandibles short and robust, with inflated bases; tip slightly hooked; first marginal tooth of left mandible near the middle and small, not extending much beyond apical cutting edge; first marginal tooth of right mandible vestigial; apical cutting edge of both mandibles evenly rounded except for notch anterior to left M1. Anterior margin of pronotum slightly emarginate; posterior margin of pronotum nearly straight; thoracic spines weakly developed and slightly upturned; lateral corners of pronotum sharp but not forming conical spines. Head capsule with scattered short, straight bristles, more numerous laterally; base of mandibles with many short hairs; postmentum with numerous short, straight bristles; pronotum with many bristles on anterior lobe and margins; meso- and metanotum with numerous bristles on posterior margin and a few on spines and lateral margins; tergites with many bristles near hind margin.

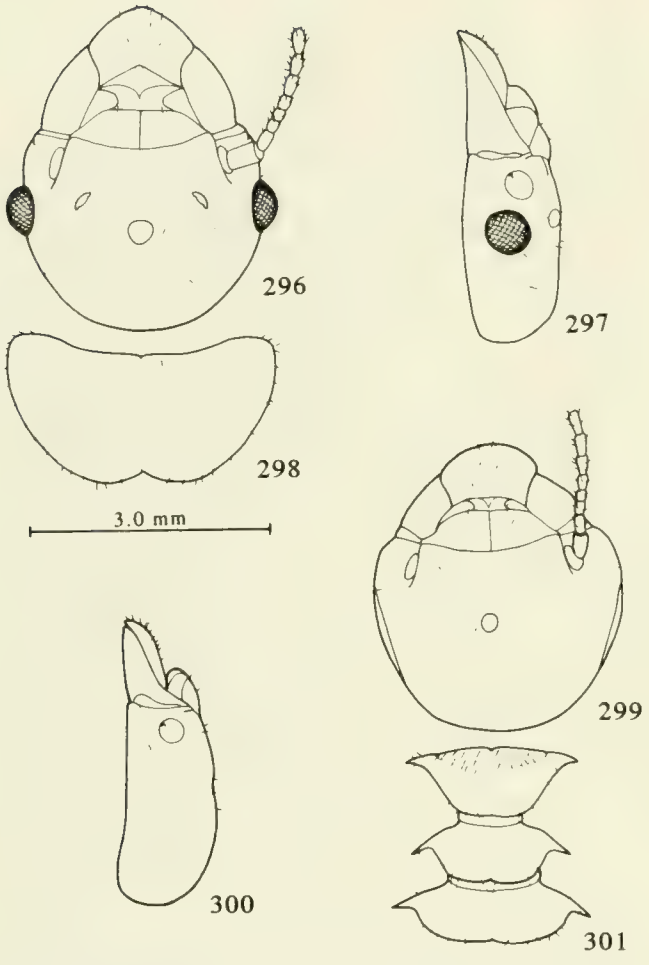


Figs. 291-295. *Syntermes territus*, soldier. 291. head, dorsal view; 292. head, lateral view; 293. thorax, dorsal view; 294. postmentum; 295. mandibles, ventral view.

Measurements (in mm) of 5 soldiers from 5 colonies: length of head 5.60-6.20; maximum width of head 4.50-5.20; height of head excluding postmentum 3.00-3.30; length of frontal tube 0.24-0.30; length of left mandible 2.40-2.55; curvature of left mandible 0.80-0.90; distance from M1 to M2 on left mandible 0.47-0.59; width of left mandible 0.76-0.82; length of left M1 0.12-0.15; minimum width of postmentum 0.77-0.94; width of pronotum 3.30-3.80; width of metanotum 3.10-3.70; length of hind tibia 4.00-4.40. Ratio length of head to maximum width of head 1.19-1.28; length of left mandible to length of head 0.41-0.43; length of hind tibia to length of head 0.68-0.77; width of pronotum to maximum width of head 0.67-0.78; distance M1-M2 to length of left mandible 0.18-0.24; height of head to maximum width of head 0.63-0.67; width to length of left mandible 0.30-0.34.

Large worker (Figs. 299-301). Head capsule with a few scattered short bristles; postclypeus with four bristles. Fontanelle rounded and small. Antenna with 19 to 20 articles. Thoracic spines moderately developed. Mandibles very similar to those of *S. longiceps*. Gut also similar to that of *S. longiceps*.

Measurements (in mm) of 4 large workers from 4 colonies: length of head 2.40-2.60; maximum width of head 2.85-3.10; length of fontanelle 0.22-0.27; width of pronotum 2.05-2.15; width of metanotum 2.15-2.55; length of hind tibia 3.65-3.90.



Figs. 296-301. *Syntermes territus*. Imago: 296. head, dorsal view; 297. head, lateral view; 298. pronotum. Large worker: 299. head, dorsal view; 300. head, lateral view; 301. thorax.

Comparisons. The alate of *S. territus* is most similar to those of *S. parallelus* and *S. longiceps*, which are smaller, with anterior corners of pronotum more distinctly angular, and only two bristles on postclypeus. The soldier can be distinguished by its elongate head with nearly parallel sides, robust mandibles with weak dentition, and weakly developed thoracic spines. Some soldiers of *S. longiceps* from central Amazonia are similar, but are smaller and with more conspicuous marginal teeth on both mandibles.

Distribution and Geographical Variation. Sparse records from Guyana to northeastern Brazil and central Amazonia (Fig. 323). Soldiers from Ceará are almost identical to those from Guyana, and apparently there is little variation. There is some size variation, but without any geographic pattern.

Biology. According to Emerson (1945), *S. territus* inhabits forests and its nest is completely subterranean.

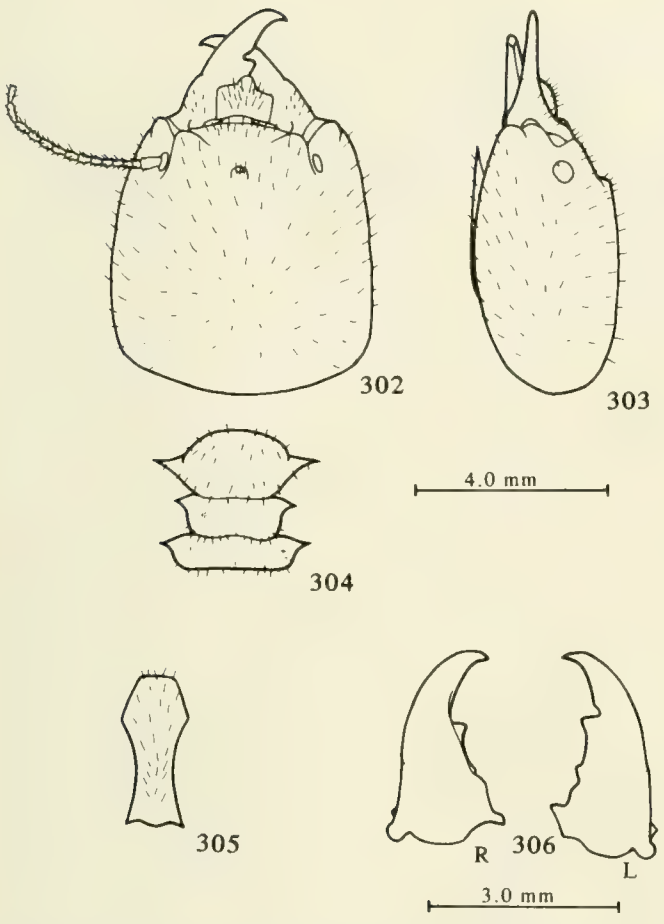
Syntermes wheeleri Emerson

Syntermes wheeleri Emerson 1945: 455, fig. 10 [soldier]. Holotype soldier: BRAZIL. "Rio, Bras.", pinned [MCZ]. Part of the type series of *S. dirus*. See comments about type locality below.

Syntermes dirus, Negret & Redford 1982, misidentification [biology, nest]; Baker et al. 1981 [chemical composition of frontal gland secretions]; Brandão 1991 [ecology].

Material examined. BRAZIL. *Bahia*. Vitória da Conquista, coll. R.L. Araujo, 30.vi.70, soldiers, workers [MZSP-4799]. *Distrito Federal*. Brasília, 20.ii.78, soldiers [UnB]; coll. A.E. Mill, 12.iv.80, soldiers, workers [MPEG-1333]; coll. A.E. Mill, 6.iii.80, soldiers, workers [two vials, BMNH]; coll. H.R. Coles, 04.ii.77, soldiers [MZSP-9301 and UnB]; coll. H.R. Coles, 08.ii.77, soldiers, workers [3 vials, UnB]; coll. H.R. Coles, 12.xii.76, soldiers [MZSP-9291]; coll. H.R. Coles, 20.x.76, soldiers [MZSP-9290]; coll. H.R. Coles, 24.iii.77, soldiers, workers [two vials, UnB]; coll. H.R. Coles, 27.i.77, soldiers [MZSP-9296 and MZSP-9299]; coll. H.R. Coles, 28.v.77, soldiers, workers [UnB]; coll. H.R. Coles, 29.iv.77, soldiers, workers [UnB]; coll. H.R. Coles, vi.77, soldiers, workers [4 vials, BMNH]; coll. H.R. Coles, xi.76, soldiers [MZSP-9292 and UnB]; coll. K. Kitayama, xii.74, soldiers, workers [MZSP-7331]; coll. M.G. Siqueira, 03.ix.82, soldiers, workers [two vials, UnB]; coll. M.G. Siqueira, 03.vi.82, soldiers, workers [five vials, UnB]; coll. R. Constantino, 02.iii.86, soldiers, workers [MPEG-2615]; coll. R. Constantino, 17.x.86, alates [MPEG-2702]; coll. R. Constantino, 24.x.86, alates [MPEG-2699]; Brasília: Fazenda Água Limpa, coll. H.R. Coles, 15.vii.77, soldiers, workers [MPEG-1269 and MPEG-1287]; coll. D. Brandão, 1981, alates [UFG-154]. *Goiás*. Anápolis, coll. H.F. Cunha, 12.vii.92, one soldier, workers [UFG-441]. Goiânia, coll. D. Brandão, 9.iii.83, soldiers, workers [UFG-4]; coll. R.F. Souza, 17.v.91, soldiers, workers [UFG-430]; coll. R.F. Souza, 06.vii.91, soldiers, workers [UFG-440]. Padre Bernardo, coll. H.R. Coles, vii.1977, four first form soldiers, workers [MZSP]. Parque Nacional das Emas, coll. K. Redford, 3.vi.80, soldiers, workers, [two vials, BMNH]. *Mato Grosso do Sul*. Três Lagoas, coll. F. Lane, vi.67, soldiers, workers [MZSP-1811]; coll. F. Lane, vi.66, soldiers, workers [MZSP-1833]. *Minas Gerais*. Barbacena, coll. F. Silvestri, 22.viii.45, soldiers, workers [LEFS]. Belo Horizonte, coll. Schreiber, vii.68, soldiers, one worker [MZSP-1808]; coll. R.L. Araujo, 28.vii.53, soldiers, workers [MZSP-4020]; coll. R.L. Araujo, 01.xi.56, soldiers, alates [MZSP-4479]; coll. D. Lavalle, 1969, one soldier, workers [MZSP-4741]; coll. F. Avila-Pires, ii.71, alates [MZSP-8567]. Bocaiuva, coll. R.L. Araujo, 25.vii.75, soldiers, workers [MZSP-5918]. Bom Sucesso, coll. R.L. Araujo, 12.xi.72, soldiers, workers [MZSP-5795]. Campanha, coll. R.L. Araujo, 28.vii.54, soldiers, workers [MZSP-4227]. Curvelo, soldiers, workers [MZSP-4439]; coll. R.L. Araujo, 14.xi.72, alates [MZSP-5595]. Diamantina, coll. R.L. Araujo, 23.viii.71, soldiers, workers [MZSP-4950 and MZSP-4955]. Guanhães, coll. R.L. Araujo, 02.iii.72, soldiers, workers [MZSP-5003 and MZSP-5004]. Lagoa Santa, coll. R.L. Araujo, 07.i.54, soldiers, workers [MZSP-4073]; coll. R.L. Araujo, 03.i.57, soldiers, workers [MZSP-4543]; coll. Reinhardt, 20.iii.89, one soldier, workers [ZMUC]. Lavras, coll. R.L. Araujo, xi.72, soldiers, workers [MZSP-5594]. Paracatu, coll. K. Kitayama, 19.ii.72, soldiers, workers [MZSP-7335]. Serra do Cipó, coll. R.L. Araujo, 04.iii.72, soldiers, workers, one alate [MZSP-5032]. Uberaba, coll. Goodland, v.65, soldiers, workers [MZSP-1171]. *São Paulo*. Artur Alvim, coll. V. Autuori, 20.vi.53, soldiers, workers [MZSP-3841]. Barueri, coll. K. Lenko, 19.vii.67, soldiers, workers [MZSP-1867]. Conceição de Itanhaém, coll. Silvestri, soldiers [MZSP-1841]. Congonhas, coll. R.L. Araujo, 26.vi.57, soldiers, workers [MZSP-3370]. Itupeva, coll. F. Mariconi, 10.xi.74, soldiers, workers, alates [MZSP-6876]. Palestina, coll. E. Amante, 27.ix.74, soldiers [MZSP-5889]. São Miguel Paulista, coll. R.L. Araujo, 31.x.50, soldiers, one worker, alates [MZSP-3261]. São Paulo, coll. H. Luederwaldt, 16.x.07, one soldier, workers, one alate [MZSP-1150]; coll. Silvestri, soldiers, workers, alates [MZSP-1834]; coll. R.L. Araujo, 31.x.50, soldiers, workers [MZSP-3259].

Imago (Figs. 312-314). Eyes moderately large, more than 1/4 width of head; ocelli small; fontanelle slightly elongate, sometimes nearly triangular. Antenna with 20 articles. Anterior cor-



Figs. 302-306. *Syntermes wheeleri*, holotype soldier (except mandibles). 302. head, dorsal view; 303. head, lateral view; 304. thorax, dorsal view; 305. postmentum; 306. mandibles, ventral view.

ners of pronotum moderately angular. Wings long (Fig. 12); distal part of media and cubitus inconspicuous. Head capsule and postclypeus with many bristles; pronotum with many hairs on outer margin and surface; tergites with many hairs from middle to posterior margin. Head chestnut-brown; pronotum light chestnut; tergites chestnut-brown; sternites light chestnut; wings hyaline, except for brownish proximal and costal areas.

Measurements (in mm) of 6 imagoes from 3 colonies: length of head 2.85-3.10; width of head without eyes 3.30-3.65; length of fontanelle 0.32-0.55; length of pronotum 2.15-2.30; width of pronotum 3.90-4.20; length of hind tibia 5.90-7.10; maximum diameter of eye 0.91-1.04; length of ocellus 0.29-0.39; length of forewing 32.00-33.00; width of forewing 7.40-7.80. Ratios: diameter of eye to width of head 0.27-0.30; length of ocellus to width of head 0.09-0.11; length of fontanelle to width of head 0.09-0.16; width of pronotum to width of head 1.12-1.23; length of wing to width of head 9.14-9.57; length of hind tibia to width of head 1.67-2.06.

Soldier (Figs. 302-306). Head capsule short, length and width of head about equal; sides converging slightly anteriorly or nearly parallel; posterior margin rounded; frontal tube very short, pore clearly visible in dorsal view; labrum short, length about equal to width; lateral corners of labrum about equal to a right angle; median lobe of labrum short. Antenna with 19 to 20 articles. Postmentum constricted near the middle, or not constricted with sides of posterior part nearly parallel. Mandibles curved and moderately elongate; tip slightly hooked; first marginal tooth of left mandible moderately large, usually extending a little beyond apical cutting edge; first marginal tooth of right mandible conspicuous; angle between right M1 and apical cutting edge about 90°; apical cutting edge of left mandible conspicuously sigmoid, forming a notch anterior to M1; apical cutting edge of right mandible evenly curved. Anterior margin of pronotum nearly rounded or slightly emarginate; posterior margin of pronotum nearly straight; thoracic spines weakly developed and upturned; lateral corners of pronotum sharp but usually not forming conical spines, although sometimes forming short spines. Head capsule with many straight bristles, more numerous laterally; postclypeus densely covered with hairs; base of mandibles with a few hairs; postmentum with numerous straight bristles; pronotum with many bristles on entire surface, more numerous on anterior lobe; meso- and metanotum with numerous bristles on posterior margin and a few on spines and lateral margins; tergites with numerous bristles on posterior half.

Measurements (in mm) of 10 soldiers from 10 colonies: length of head 5.10-5.90; maximum width of head 5.10-5.80; height of head excluding postmentum 2.80-3.10; length of frontal tube 0.15-0.25; length of left mandible 2.80-3.00; curvature of left mandible 0.80-1.10; distance from M1 to M2 on left mandible 0.59-0.76; width of left mandible 0.76-0.92; length of left M1 0.18-0.31; minimum width of postmentum 0.81-0.96; width of pronotum 3.10-3.80; width of metanotum 3.30-4.00; length of hind tibia 4.70-5.30. Ratio length of head to maximum width of head 0.98-1.12; length of left mandible to length of head 0.49-0.56; length of hind tibia to length of head 0.82-0.93; width of pronotum to maximum width of head 0.60-0.70; distance M1-M2 to length of left mandible 0.21-0.25; height of head to maximum width of head 0.53-0.59; width to length of left mandible 0.27-0.31.

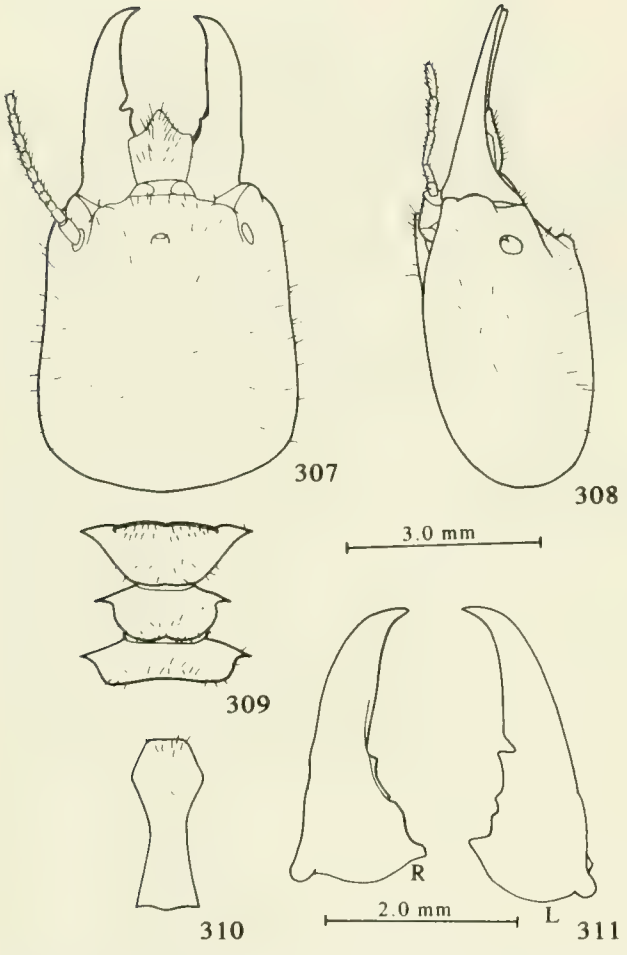
First form soldier (Figs. 307-311). Smaller than the normal soldier and with more elongate head and mandibles; smaller marginal teeth closer to the base on both mandibles.

Measurements (in mm) of 3 soldiers from 1 colony: length of head 4.45-4.80; maximum width of head 3.90-4.30; height of head excluding postmentum 2.30-2.55; length of frontal tube 0.17-0.22; length of left mandible 2.70-2.85; curvature of left mandible 0.80-0.95; distance from M1 to M2 on left mandible 0.44-0.47; width of left mandible 0.71-0.77; length of left M1 0.13-0.17; minimum width of postmentum 0.67-0.74; width of pronotum 2.45-2.80; width of metanotum 2.60-2.70; length of hind tibia 4.50-4.75. Ratio length of head to maximum width of head 1.12-1.17; length of left mandible to length of head 0.57-0.61; length of hind tibia to length of head 0.94-1.01; width of pronotum to maximum width of head 0.63-0.65; distance M1-M2 to length of left mandible 0.16-0.17; height of head to maximum width of head 0.59-0.62; width to length of left mandible 0.26-0.28.

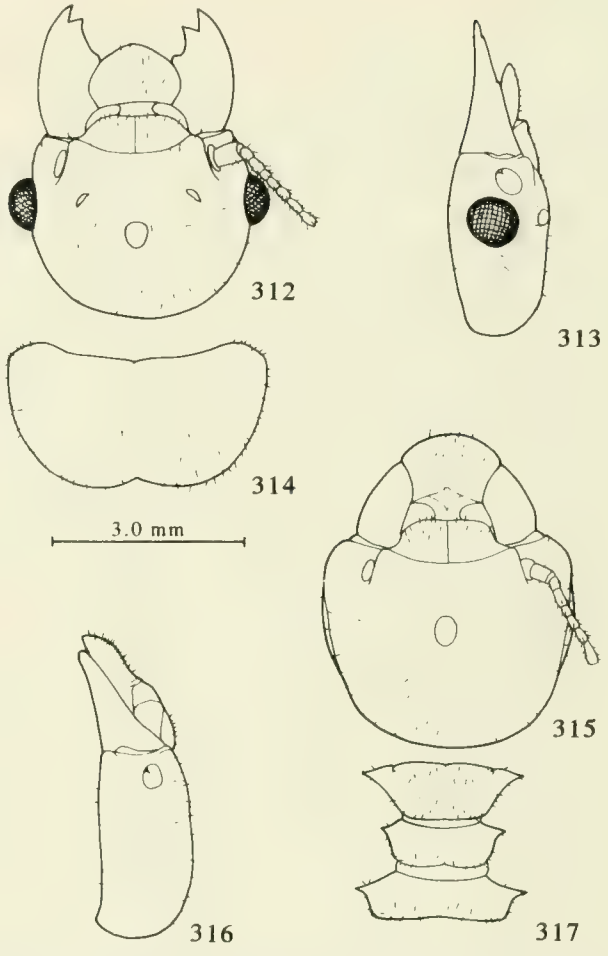
Large worker (Figs. 315-317). Head capsule and postclypeus densely covered with short, straight bristles. Fontanelle slightly elongate and moderately large. Antenna with 19 to 20 articles. Thoracic spines weakly developed. Mandibles very similar to those of *S. grandis*, with broad molar plate. Gut (Figs. 28-34) very large, with strongly inflated 1st and 3rd segments of hindgut; mixed segment with major midgut prolongation very large and wide, and minor prolongation rounded, small, and slightly inflated.

Measurements (in mm) of 5 large workers from 5 colonies: length of head 3.05-3.20; maximum width of head 3.50-3.73; length of fontanelle 0.25-0.39; width of pronotum 2.20-2.55; width of metanotum 2.40-2.70; length of hind tibia 4.15-4.40.

Comparisons. The alate is similar to that of *S. peruanus*, but is larger. Alates of *S. grandis* and *S. magnoculus* are also superficially similar, but are usually larger and have proportionally larger eyes and ocelli, and a rounded fontanelle. The soldier of *S. wheeleri* is



Figs. 307-311. *Syntermes wheeleri*, first form soldier. 307. head, dorsal view; 308. head, lateral view; 309. thorax, dorsal view; 310. postmentum; 311. mandibles, ventral view.



Figs. 312-317. *Syntermes wheeleri*. Imago: 312. head, dorsal view; 313. head, lateral view; 314. pronotum. Large worker: 315. head, dorsal view; 316. head, lateral view; 317. thorax.

most similar to that of *S. obtusus*, which has the first marginal tooth of the right mandible vestigial and a smaller tooth on the left mandible. Soldiers of *S. grandis* are usually larger, with larger marginal teeth on both mandibles and a more strongly sigmoid apical cutting edge of the left mandible, but there is considerable variation and possibly some overlap. I was not able to find a good external character to separate the soldier of *S. grandis* from *S. wheeleri*, but they may be easy to identify based on nest differences.

Distribution and Geographical Variation. Central and southeastern Brazil, in the southern portion of the cerrado region (Fig. 325). Soldiers show considerable morphological variation, but there is no clear geographic pattern.

Biology. *S. wheeleri* lives in the cerrado and some areas of grassland. Its nest (Fig. 3) is described in the section on nests above.

Remarks. Araujo (1977: 6), based on the study of non-type material, erroneously concluded that *S. wheeleri* was a synonym of *S. dirus*. These two species are quite distinct, except for a very superficial similarity of soldiers. Apparently Araujo arrived at his conclusion based on the fact that the type locality is the same for both species (Rio de Janeiro), and he was not able to find *S. wheeleri* there, after years of observation and collecting. However, I suspect that the label information of the type specimen may be incorrect. *S. wheeleri* is clearly a cerrado and grassland species, a kind of habitat not present in the vicinity of Rio de Janeiro. The first form soldier was described from material not collected with normal soldiers and there is no direct information on the age of the colony. Therefore, it is possible that it actually belongs to a different species. However, it seems to fit the morphological pattern of first form soldiers, the material was collected in a region where *S. wheeleri* is abundant, and the workers are identical to those of *S. wheeleri*, including gut morphology.

PHYLOGENETIC RELATIONS OF THE SPECIES OF *SYNTERMES*

Emerson (1945: 441) briefly discusses the phylogenetic relationships of the genus *Syntermes*, claiming that it is the most primitive member of the Nasutitermitinae, a position maintained in all traditional phylogenies. Both Holmgren (1912: 47) and Emerson (1945) advocate a relationship

between *Syntermes* and the macrotermitine genus *Acanthotermes*, based primarily on the common presence of thoracic spines in the soldier caste. The latter hypothesis seems to have supported the idea of a sister group relationship between the Nasutitermitinae and the Macrotermitinae. However, these hypotheses are not supported by a formal cladistic analysis (Constantino, in prep.), the Macrotermitinae seem to form a separate clade in relation to all other members of the family Termitidae, and *Syntermes* is probably not the most basal lineage of the Nasutitermitinae, apparently forming a clade with the genera *Cornitermes*, *Procornitermes*, *Labiotermes* and *Paracornitermes*. Among the characters mentioned by Emerson (1945) as evidence for the primitiveness of *Syntermes* and its putative relationship with *Acanthotermes*, some can be dismissed because they were based on grades (for Emerson, some characters were always primitive, e.g. large size). The evidence against the hypothesis of homologous thoracic spines in *Syntermes* and *Acanthotermes* is: 1) not all species of *Syntermes* bear spines; 2) the spines are in different positions in the two genera, specially on the pronotum; 3) *Pseudacanthotermes*, which is clearly closely related to *Acanthotermes*, lacks the lateral spines; 4) other characters, specially the digestive tube, indicate a distant relationship between these two genera. The short R_1 joining the costal border, mentioned by Emerson as a primitive character in *Syntermes*, is also present in many related genera, although it may be difficult to detect in small species. The presence of a third apical spur on the foretibia is the only character that could possibly indicate that *Syntermes* is the basal lineage of the Nasutitermitinae, if the loss of this spur is a synapomorphy for the rest of the subfamily. The problem with this hypothesis is that some species of *Procornitermes*, a closely related genus, have three spurs on the foretibia; this character is also somewhat variable in other groups of termites.

No hypothesis about the phylogenetic relationships among the species of *Syntermes* has ever been proposed, except for some vague comments included in taxonomic descriptions. The number of valid species recognized in this work is 23, six of them known from soldiers and workers only. Within the limitations of the material available for study, the morphology of all the species of *Syntermes* was exhaustively studied. Unfortunately, there is much missing information for many species, which resulted in many question marks in the data matrix and certainly reduced resolution.

I included as many characters as possible, excluding only obvious autapomorphies and characters that seemed too variable to be phylogenetically informative. Some of the included characters show no variation in *Syntermes*, but they provide information about the relationship of *Syntermes* to the outgroup taxa, and of outgroup taxa to one another. Multi-state characters were coded as additive when the various states could clearly be ordered in an evolutionary sequence, and coded as non-additive when order was unclear.

The choice of the outgroup was based on my analysis of the subfamily Nasutitermitinae (Constantino, in prep.), which indicated that *Syntermes* is closely related to *Cornitermes*, *Labiotermes*, *Paracornitermes* and *Procornitermes*. *Paracornitermes* was not included because it is so close to *Labiotermes* that most characters would be identical, and increasing the number of taxa would make the analysis more time-consuming. Data on the outgroups were obtained from Emerson (1952), Emerson & Banks (1965), Kovoor (1969), Cancello (1986), and Cancello (1989).

The present analysis included 26 taxa and 45 characters, 21 from soldiers, 10 from imagoes, 12 from workers, and 2 behavioral / ecological (Table 2), and was performed with the computer programs Hennig86 1.5 (Farris, 1988) and Pee-Wee 2.1 (Goloboff, 1993; 1994). Hennig86 searches for most parsimonious trees, i.e., trees with minimum number of steps or evolutionary changes using equal or pre-defined weights for characters. It also performs successive weighting, an iterative procedure in which character weights are determined by the degree of homoplasy of each character in most parsimonious tree(s) previously found. The process of setting weights and searching for shortest trees is repeated until a stable solution is found. Goloboff (1993) pointed out several problems with the successive approximations approach, and proposed the use of implied weights, a non-iterative procedure that estimates character reliability and sets weights during tree search. This procedure is implemented in Pee-Wee, a program that searches for trees with best character fit. In Hennig86 the function mh* was initially used to produce trees, which were submitted to branch-swapping bb*. Successive approximations were performed with the function xs w, followed by bb*; this process was repeated until the result became stable. In Pee-Wee, the option mult*15 was used, followed by max* and jump if necessary. Character analysis distributions shown in the cladograms (Figs. 326-331) were determined with the computer program Clados 1.2 (Nixon, 1992). The following analyses were performed:

Analysis 1A included all taxa and used Hennig86. Four trees of length 124, consistency index (ci) 50, and retention index (ri) 76 were found.

Analysis 1B was made by applying successive weighting to the results of analysis 1A, and resulted in a single tree of length 444, ci= 69, and ri= 87.

Analysis 1C was made using Pee-Wee. It resulted in a single tree of fit= 335.5.

Analysis 2A was performed like 1A but included only the species with known alates, thus reducing the number of question marks in the data matrix. Species excluded are *S. barbatus*, *S. bolivianus*, *S. brevimalatus*, *S. calvus*, *S. crassilabrum*, *S. insidians*. It resulted in three trees of length 109, ci= 56, ri= 78.

Analysis 2B was like 1B but with the smaller matrix. It resulted in two trees of length 450, ci= 78, and ri= 91.

Analysis 2C used Pee-Wee and the smaller matrix. It resulted in a single tree of fit 355.2.

Figs. 318-321. Known geographical distributions of *Syntermes* species. The dotted line indicates the limits of distribution for the genus.

LIST OF CHARACTERS

Soldier

1. Left mandible with: (0) M1 close to M2 (Figs. 197, 235). (1) M1 distant from M2 (Figs. 58, 141, 254).

2. Cutting edge between M1 and M2 on left mandible: (0) Not serrated (all *Syntermes* species). (1) Serrated (*Cornitermes* and *Procornitermes*).

3. Left mandible: (0) With a notch anterior to M1 (Figs. 125, 197, 306. (1) Without a notch anterior to M1 (Figs. 58, 69).

4. Molar plate and molar prominence: (0) Vestigial. (1) Absent.

Figs. 322-325. Known geographical distributions of *Syntermes* species. The dotted line indicates the limits of distribution for the genus.

Soldier mandibles of all *Syntermes* and *Labiotermes* species have very reduced but conspicuous molar regions. In soldiers of *Cornitermes* and *Procornitermes* this structure is not visible.

5. Mandibles: (0) Moderately elongate (Figs. 58, 141). (1) Short and robust. (2) Slender and elongate (Figs. 197, 284). Coded as non-additive because evolutionary order is unclear.

6. Tip of mandibles: (0) Slightly or not hooked (Figs. 58, 77). (1) Strongly hooked (Figs. 197, 208).

7. Left M1: (0) Small, not extending beyond apical cutting edge (Figs. 77, 219). (1) Large (Figs. 58, 141).

8. Right M1: (0) Small (Figs. 77, 170). (1) Large (Figs. 58, 125, 141). (2) Vestigial (Figs. 197, 284). Coded as non-additive.

9. Angle between right M1 and longitudinal axis of mandible: (0) About 90 degrees (Figs. 101, 117). (1) Less than 90 degrees (Figs. 58, 141). (2) More than 90 degrees (219, 295). Coded as non-additive.

10. Base of mandibles: (0) Not inflated (Fig. 77). (1) Inflated (Fig. 69).

11. Head size: (0) Small (length of head x width of head less than $20mm^2$). (1) Medium ($20 - 35mm^2$). (2) Large (more than $35mm^2$). Coded as additive. This character was included in this analysis because the large size of most *Syntermes* species seems to be a derived condition. Emerson (1945) argued that large size is primitive.

12. Head capsule: (0) Elongate (Fig. 166). (1) Short (Fig. 54).

13. Sides of head: (0) Nearly parallel (Figs. 204, 231). (1) Converging anteriorly (Figs. 54, 193).

14. Frontal tube: (0) Very short, pore visible from dorsal view (Figs. 193, 242). (1) Short, pore not visible from dorsal view (Figs. 54, 231). (2) Moderately elongate (*Cornitermes* and *Procornitermes*). Coded as additive.

15. Soldier antenna with: (0) 13-16 articles. (1) 19 articles. (2) 20-21 articles. Coded as additive. The number of antennal articles sometimes show intra-specific variability and is difficult to code. Nevertheless I believe it has some phylogenetic information since some species consistently have 19 articles, while other have 20-21. The few species with antenna variable in the range 19-20 were coded as variable (question mark in the matrix). Only one species has only 21 articles and none vary from 19 to 21. Most have either 19 or 20-21.

16. Sides of thoracic nota: (0) Rounded (*Cornitermes, Labiotermes*, and *Procornitermes*). (1) Moderately angular (Fig. 195). (2) Distinctly angular and sharp; sides of pronotum not ending in conical spines (Figs. 139). (3) With distinct conical spines in all segments (Figs. 56). Coded as additive.

17. Lateral projections of meso- and metanotum: (0) Horizontal. (1) Slightly upturned. (2) Strongly upturned. Codded as additive.

18. Head capsule: (0) Without long, fine, curly hairs. (1) With long, fine, curly hairs (Figs. 54, 65).

19. Head capsule: (0) Without numerous short, straight hairs. (1) With numerous short, straight hairs (Figs. 102, 250).

20. Clypeal region with: (0) 4 hairs (Fig. 204). (1) Many hairs.

21. Hairs on posterior surface of pronotum: (0) Absent (Fig. 195). (1) Present (Fig. 67).

Imago

22. Eyes: (0) Large (Figs. 198, 225). (1) Small (Figs. 131, 236).

23. Ocelli: (0) Large (Fig. 187). (1) Small (Fig. 312).

24. Fontanelle: (0) Rounded or elliptic (Fig. 59). (1) Nearly triangular (Fig. 255).

25. Anterior corners of pronotum: (0) Rounded (Fig. 200). (1) Moderately angular (Fig. 314). (2) Angular with sharp points oriented laterally (Fig. 61). (3) Angular with sharp points oriented anteriorly (Fig. 178). Coded as nonadditive.

26. Wings: (0) Hyaline. (1) Brown.

27. Wings relatively: (0) Short. (1) Long. Wings with length less than 9 times width of head were considered short.

28. Head capsule with: (0) Fairly long hairs. (1) Very short hairs. These very short hairs are present in *S. aculeosus, S. cearensis* and *S. dirus*, and are barely visible under a magnification of 60x.

29. Head capsule with: (0) Few hairs (Fig. 59). (1) Many hairs (Fig. 107).

30. Postclypeus with: (0) 4 hairs (Fig. 296). (1) 2 hairs (Fig. 236). (2) Many hairs (Fig. 147). Coded as non-additive.

31. Surface of pronotum with: (0) No hairs or a few scattered hairs (Fig. 133). (1) Numerous hairs (Fig. 227).

Worker

32. Molar plate: (0) Moderately wide. (1) Very wide.

33. Cutting edge between M_{1+2} and M_3 on left mandible: (0) Perfectly straight (Fig. 14). (1) Slightly undulated (Fig. 22).

34. Cutting edge M1 - M3 on left mandible: (0) Parallel to the line M3 - A (Fig. 18). (1) Forming an angle to the line M3 - A (Fig. 20).

35. Apical tooth of left mandible: (0) Not reduced (Fig. 14). (1) Reduced (Fig. 22).

36. Proximal border of the apical ridge of molar plate: (0) Slightly concave. (1) Strongly concave. The first ridge (most distal, also called apical thickening) of the molar plate is distinctly more curved in some species of *Syntermes*.

37. Major prolongation of mixed segment: (0) Tongue-shaped (Fig. 39). (1) Nearly circular with constricted connection to midgut (Fig. 36). (2) Elongate with nearly rectangular tip (Fig. 45).

38. Tip of major prolongation of mixed segment: (0) Not inflated. (1) Inflated. In some species the major mesenteric prolongation of the mixed segment is distinctly swollen, while in most species it is flat.

39. Minor prolongation of mixed segment: (0) Elongate longitudinally (Fig. 52). (1) Shaped like a golf club, enlarged towards the Malpighian tubules (Fig. 39) (2) Elongate transversely, with constricted connection to midgut (Fig. 36). (3) Small, circular, and inflated (Fig. 33). Coded as non-additive.

40. Widening of the gut in the mixed segment: (0) Gradual (Figs. 52-53). (1) Abrupt (Figs. 45-47). In most species the mixed segment widens gradually towards the hindgut. In *S. longiceps, S. parallelus*, and *S. territus* the first part of the mixed segment is nearly cylindrical, about the same width as the midgut, and enlarges suddenly into a pouch.

41. Enteric valve located on: (0) Posterior left side (Figs. 31). (1) Posterior right side (Figs. 41-44). In *S. longiceps, S. parallelus*, and *S. territus* the gut has a distinct arrangement, with a larger first segment of the hindgut, pushing the location of the enteric valve to the other side of the abdomen.

42. Enteric valve: (0) With sclerotized armature. (1) Without sclerotized armature. The absence of spines on the enteric valve is characteristic of all *Syntermes*. The primitive condition seems to be the presence of six plates (or swellings) with numerous sclerotized spines.

43. Enteric valve: (0) Narrow. (1) Very wide. All *Syntermes* species have a very wide enteric valve; in other genera the gut is much more constricted near the valve.

Behavior and Ecology

44. Nest: (0) Completely subterranean (Fig. 4). (1) Mostly subterranean with a pile of loose soil above ground (Fig. 2). (2) Epigeal and compact (Fig. 3). (3) Mostly subterranean with a soft, flat, epigeal portion. Coded as non-additive because order is unclear; nest of type (2) could have evolved from type (1), but it could also have originated from a type (0). This is still a crude classification of the nests of *Syntermes*, but it carries some information.

45. Habitat: (0) Savanna. (1) Forest. Habitat fidelity seems to be high in *Syntermes*, and no species is known to live in both kinds of habitats. Habitat association involves differences in diet (grass-litter or leaf-litter) and probably also adaptations to different microclimates and biological interactions (e.g. with predators).

RESULTS AND DISCUSSION

Analysis 1A resulted in four different trees, but there are basically two distinct topologies (Figs. 326 and 327). The other two trees, which are not illustrated, differ only in the relative position of *S. wheeleri, S. bolivianus* and *S. peruanus* and are otherwise identical to the tree shown in Fig. 327. Although few trees were found in this analysis, they are quite different in the mid-level branching and therefore the

TABLE 2. Matrix of character states.

	1 1 2 2 3 3 4 4 5 0 5 0 5 0 5 0 5
Labiotermes	00002000000?10000??00??00000?11⊥10000?0000??
Cornitermes	01012000000?20000???0000??0?21?0?000000000??
Procornitermes	010120000000200000?0?1000101??11100?0?0100??
aculeosus	10100011102111?32101111021010200010100?001111
barbatus	10101111212101121101 1??????????00100102001100
bolivianus	10000000201100122001 1??????????10000????11?0
brevimalatus	10101111212001121001 0??????????00100????11?1
calvus	10000001201111?320010??????????00100000011?1
cearensis	10000001001101232 10?11102111020001010010011 11
chaquimayensis	100000?1102111?32011111021101200010100?001111
crassilabrum	10101?110121?11220010??????????00100001001 1?1
dirus	100000?10021112321011110211102000101001001111
grandis	10000011102110222001100010101211000000000 01130
insidians	1000001110000122100 11??????????00100001001100
longiceps	?00000?0?0?00112100101103100010001002101111?1
magnoculus	10100011102110222001100010101211000000000 11?0
molestus	00002102?000101100000000000101000111001000 1101
nanus	00002102?000001100000000000101000111001000 1100
obtusus	?00000002021??22200110011010121100000010011 00
parallelus	00000000200001121001011031000100010021011 11?1
peruanus	100000?0201110?32001101110101 21???00?????1120
praecellens	10101111011001121011111110101210010010200 1100
spinosus	10000011102111?32011111021100200010100 1001111
tanygnathus	00002002202111232001111021100000010000000 1111
territus	?000000021100112100001101100000001002101111 01
wheeleri	100000?1001110?22001101110101211000000 3001120

strict consensus tree (Fig. 328) shows a large polytomy.

The application of successive weighting (analysis 1B) to the results of analysis 1A resulted in a single tree, very similar to the one in Fig. 326. The only difference was a reversal in the relative position of *S. tanygnathus* and *S. calvus*. The use of implied weights (analysis 1C) also generated a single tree, with groups of species similar to those found in analyses 1A and 1B, but with a major difference in the position of these groups (Fig. 329).

Analysis 2A included only the species with known alates, and resulted in three different trees. The strict consensus tree is shown in Fig. 330. The differences among the three trees are in the relative position of *S. grandis*, *S. magnoculus* and *S. obtusus*. The basic topology of these trees is stable to successive approximation (analysis 2B), which resulted in two trees, one of them identical to their strict consensus tree (Fig. 331). Analysis 2C, with implied weights, resulted in a single tree, identical to the strict consensus of analysis 2B (Fig. 331).

Although the results of different analyses show some variation, several groups are stable and seem to be well supported. The *molestus* group, with two species, is clearly monophyletic and consistently appears as the most basal branch of *Syntermes*. The main characters supporting this group are: (6-1) the strongly hooked soldier mandible; (8-2) marginal dentition reduced on both mandibles; (35-1) reduced apical tooth of the worker mandibles; and (38-1) the inflated major mesenteric prolongation of the mixed segment.

The *parallelus* group, including three species, is also very well supported, particularly by a distinctive gut pattern (characters 37-1, 38-1, 40-1 and 41-1). Some imago characters are derived only under some tree topologies, but at least one is constant, the very short wings (27-0). *S. parallelus* consistently appears as the sister species of *S. longiceps*, a relationship supported by two imago characters: (25-3) the shape of the pronotum, and (30-1) the presence of only two hairs on the postclypeus.

The *grandis* group includes six savanna species. Although this group is stable in all analyses, most characters supporting it are not constant. Two characters of the worker

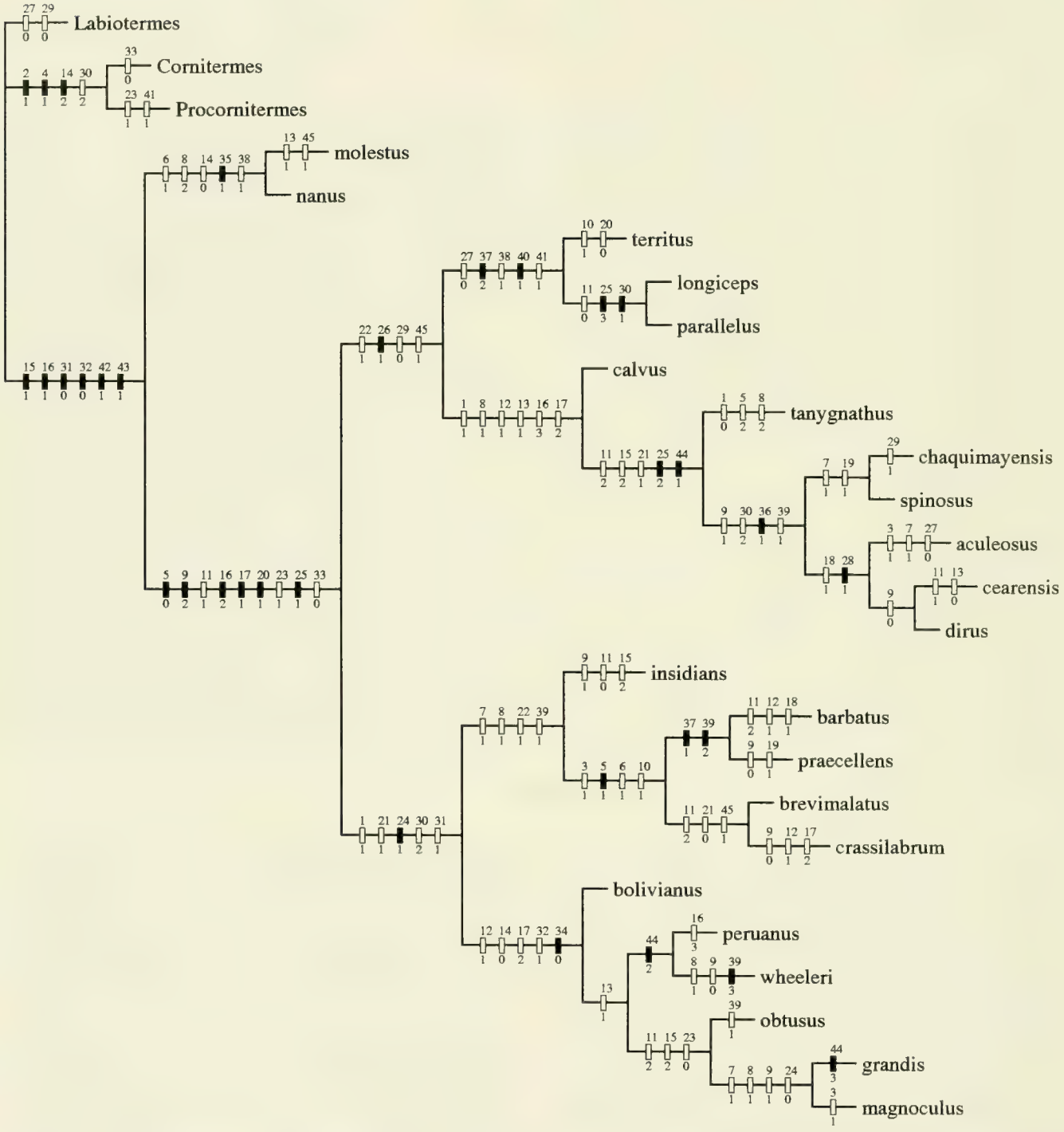


Fig. 326. Tree from analysis 1A. All species included; equal weights for all characters. Length= 124, ci= 50, ri= 76. Numbers above each branch refer to characters as defined in text; numbers below each branch refer to character states. Black bars indicate character states that are unique and unreversed within the clade subtended by the branch; white bars indicate characters that originate more than once on the tree or undergo reversal within the clade subtended by the branch.

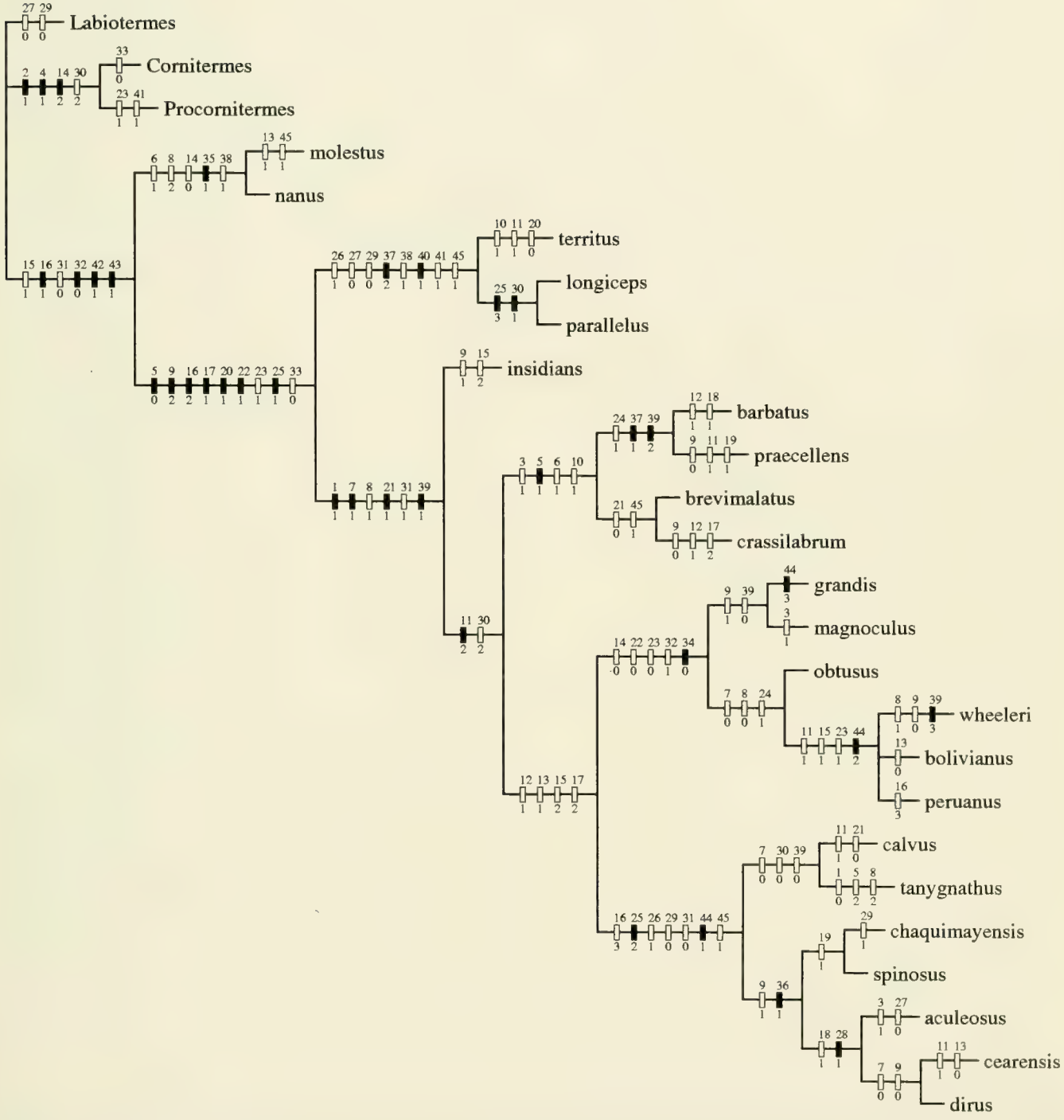


Fig. 327. Another tree from analysis 1A. All species included; equal weights for all characters. Length= 124, ci= 50, ri= 76. Symbols for characters and their states as in Fig. 326.

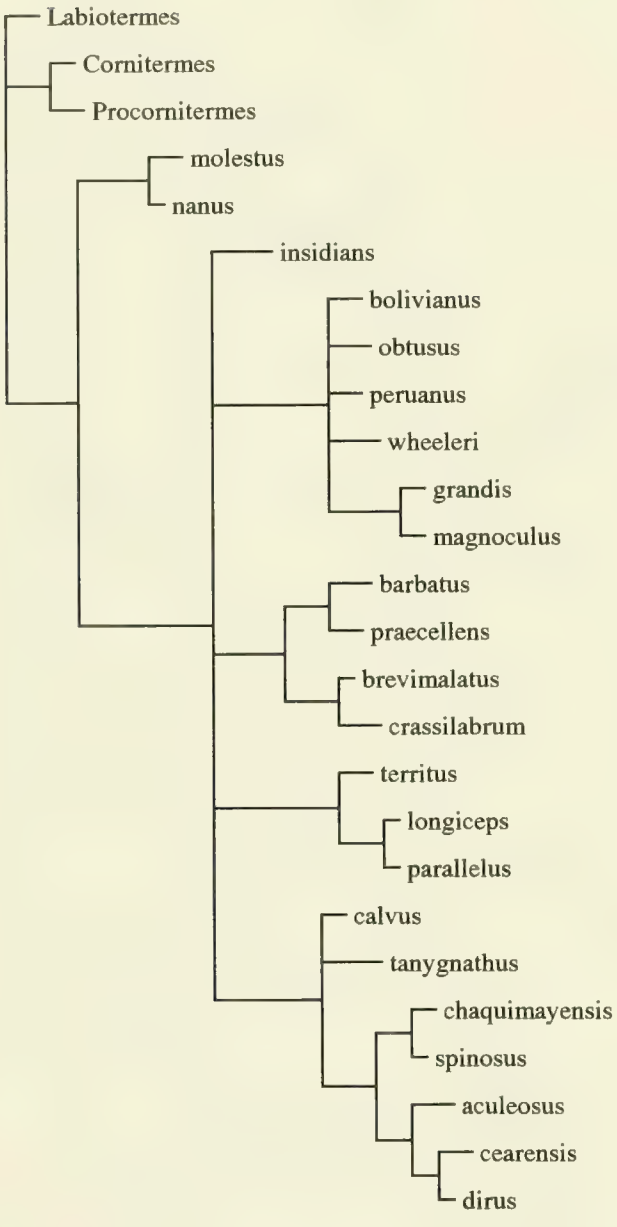


Fig. 328. Strict consensus tree from analysis 1A. All species included, equal weights for all characters.

mandibles are always present: (32-1) the broad molar plate and (34-0) the orientation of the cutting edge of left mandible. The relationships among the various species in this group are not clear. A sister group relationship between *S. wheeleri* and *S. peruanus* appears in several trees, and is supported by a similar nest type (44-2). *S. grandis* and *S. magnoculus* are other possible sister species. There are many unknown character states in this group, particularly for *S. peruanus* and *S. bolivianus*, which is one of the causes of the low resolution.

The *dirus* group contains six species, is well supported, and all species relationships are stable, except for the position of *S. tanygnathus*. It is not clear whether *S. calvus* belongs to this group or not, since the alate of that species is unknown. All species in this group have similar imagoes, with small eyes and ocelli, dark wings (26-1), and anterior corners of pronotum distinctly angular (25-2); also, they are all forest species (45-1), build similar nests (44-1), and the soldiers have large thoracic spines (16-3). The polarity of the imaginal characters varies with tree topology, but some are probably derived. The nest type and the large thoracic spines of soldiers appear as derived in all trees. The group of five species excluding *S. tanygnathus* is supported by two characters: (36-1) a strongly convex apical ridge of the molar plate of the worker mandible, and (39-1) a minor mesenteric prolongation of the mixed segment shaped like a golf club. The sister-group relationship between *S. spinosus* and *S. chaquimayensis* is consistently supported by a single character, the presence of dense, short, straight hairs on the soldier head (19-1). The group *dirus* + *aculeosus* + *cearensis* is supported by two characters: (18-1) long, fine, curly hairs on soldier head, and (28-1) very short hairs on imago head. The sister-group relationship between *dirus* and *cearensis* is supported by a similar marginal tooth on left soldier mandible (9-0).

The four species of the *brevimalatus* group are characterized by very robust and short soldier mandibles (5-1) with inflated bases (10-1), more or less hooked tips (6-1), and no notch anterior to M_1 (3-1). A sister-group relationship between *S. praecellens* and *S. barbatus* is supported by a distinctive configuration of the mixed segment (37-1 and 39-1). *S. brevimalatus* and *S. crassilabrum* are also stable as sister species, but this relationship should be treated with caution because there are many unknown character states for both species, and they share no clear synapomorphy.

The position of *S. insidians* is uncertain. It appears associated with the *brevimalatus* group in many trees, but there is no clear synapomorphy supporting the inclusion of *insidians* in any group. Hopefully, the imago of *insidians* will provide some informative characters, but it is not known yet.

One of the sources of conflict in the mid-level branching seems to be a set of imaginal characters common to the *parallelus* and *dirus* groups, which include small eyes and ocelli (22-1), dark wings (26-1), and few hairs on head capsule (29-0). Imaginal characters would favor a tree topology similar to that in Fig. 326. On the other hand, soldier characters would indicate a different position of the *S. territus* group, as in Fig. 327.

The fact that analysis 2, including only the species with known imagoes, resulted in a tree distinct from the ones obtained in analyses 1B and 1C can may be interpreted in two different ways. The many unknown character states of the species with unknown imagoes could cause the programs to converge to incorrect trees. In this case the tree in Fig. 331 would be closer to reality. It should be noted that the trees from analysis 2 are compatible with one of the trees from analysis 1A (Fig. 327). Another possibility is that the

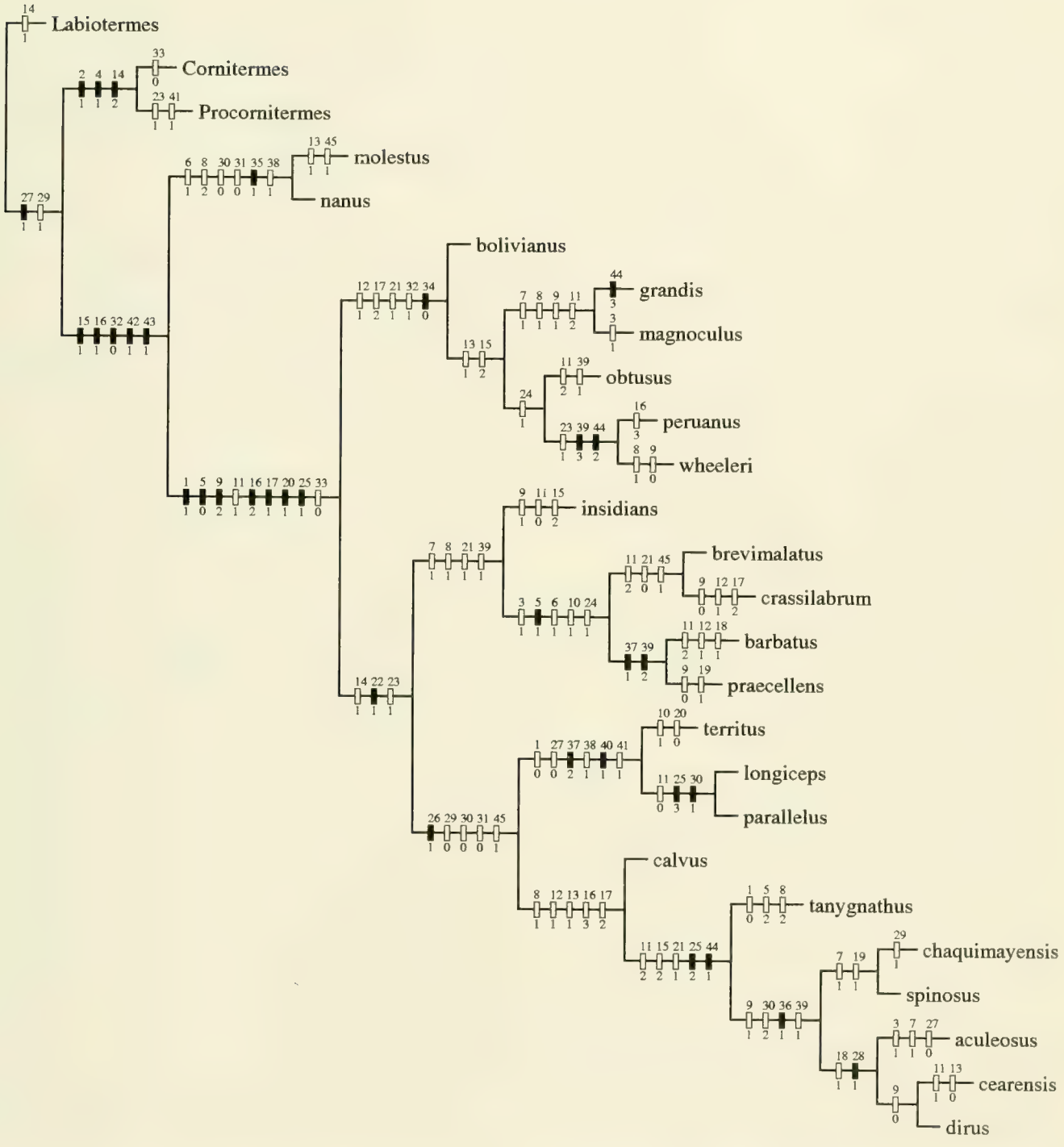


Fig. 329. Single tree from analysis 1C. All species included; implied weights using Pee-Wee. Fit= 335.5. Symbols for characters as in Fig. 326.

removal of several species would reduce information by eliminating some intermediate states or combinations of characters. If this is true, then the intermediate branching should be considered unknown, as in Fig. 328. This phylogeny will certainly be improved with more data, as soon as the unknown imagoes are described and more information on nests and biology is accumulated.

An interesting question is how many times there was a

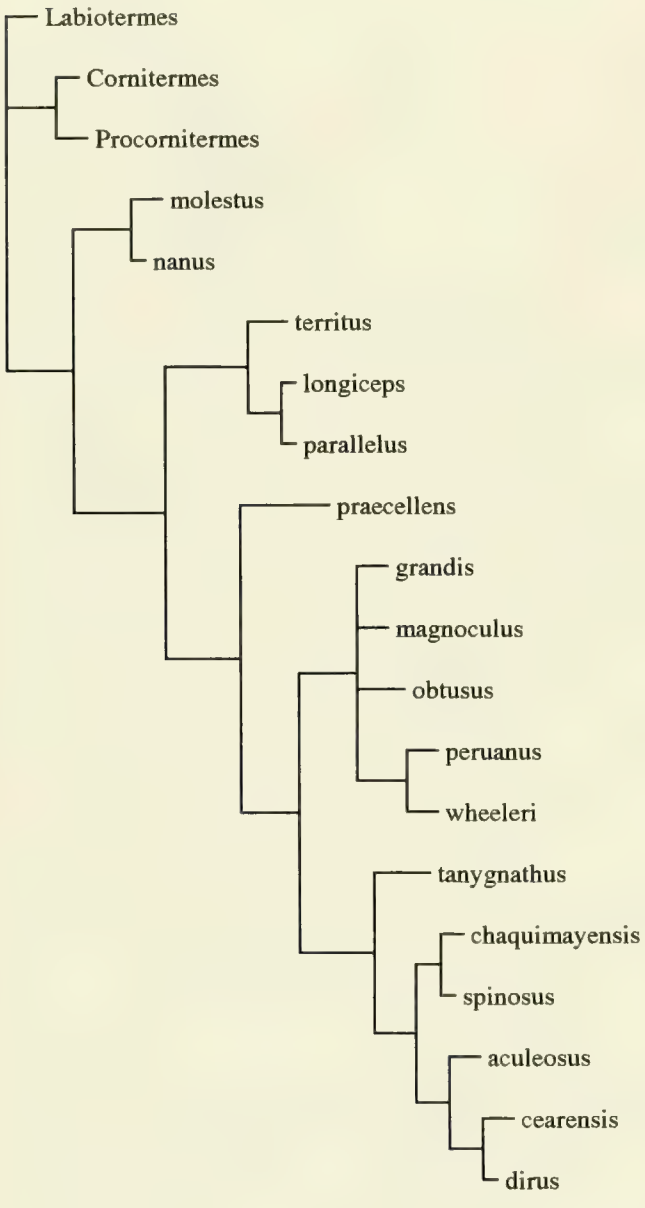


Fig. 330. Strict consensus tree from analysis 2A. Only species with known imagoes included; equal weights for all characters. From three different trees of length 109, ci= 56, ri= 78.

change in habitat, from savanna to forest or vice-versa. However, the polarity of this character (designated as 45 on the cladograms) is unclear because all outgroup genera have both savanna and forest species. And the most basal lineage, the *molestus* group, has one savanna and one forest species. The results indicate three or four changes, depending on the tree topology, either considering savanna or forest as the primitive habitat. The trees in Figs. 326-331 show only the character distribution considering savanna as the ancestral habitat, i.e., 45-1 on a branch indicates a change from savanna to forest habitat.

The large size and the thoracic spines of soldiers of *Syntermes*, which were considered by Emerson (1945) as primitive characters, consistently appear as derived characters in some species of the genus, and cannot even be considered diagnostic for *Syntermes*.

LITERATURE CITED

Araujo, R.L. 1958. Contribuição à biogeografia dos termitas de Minas Gerais, Brasil. Arquivos do Instituto Biológico 25: 219-236.

Araujo, R.L. 1977. Catálogo dos Isoptera do Novo Mundo. 92p. Rio de Janeiro: Academia Brasileira de Ciências.

Baker, R.; H.R. Coles; M. Edwards; D. Evans; P. Howse & S. Walmsley. 1981. Chemical composition of the frontal gland secretion of *Syntermes* soldiers (Isoptera, Termitidae). Journal of Chemical Ecology 7: 135-145.

Bandeira, A.G. 1991. Térmites (Insecta: Isoptera) consumidores de liteira na Ilha de Maracá, Roraima. Acta Amazonica 21: 15-23.

Barbosa, R.I. 1993. Período de forrageamento de duas espécies de *Syntermes* (Isoptera, Termitidae) em uma floresta tropical amazônica e a relação com temperatura e umidade do ar. Revista Brasileira de Entomologia 37: 763-767.

Bequaert, J. 1925. Neotermes injurious to living guava tree, with notes on other Amazonian termites. Entomological News 36: 289-294.

Blanchard, C.E. 1840. Histoire Naturelle des Insectes: Orthoptères, Naevroptères, Haemiptères, Hymaenoptères, Laepidoptères et Diptères. Pp. 46-47. Paris: P. Dumaenil.

Borgmeier, T. 1930. Eine neue termitophile Histeridengattung aus Brasilien. Zoologischer Anzeiger 88: 33-39.

Borgmeier, T. 1935. Eine neue augenlose termitophile Phoride aus Brasilien, nebst Beschreibung einer neuen Pheidolomyia (Dipt. Phoridae). Revista de Entomologia (Rio de Janeiro) 5: 488-495.

Borgmeier, T. 1959. Vier neue Gattungen und einige neue Arten termitophiler Staphyliniden aus Costa Rica und Brasilien (Coleoptera, Staphylinidae). Studia Entomologica 2: 289-308.

Bown, T.M. & J.H. Laza. 1990. A Miocene termite nest from southern Argentina and its paleoclimatological implications. Ichnos 1: 73-79.

Brandão, D. 1991. Relações espaciais de duas espécies de *Syntermes* (Isoptera, Termitidae) nos cerrados da região de Brasília, DF, Brasil. Revista Brasileira de Entomologia 35: 745-754.

Burmeister, H. 1839. Handbuch der Entomologie, Vol. 2, Part 2. Pp. 758-768. Berlin: Reimer.

Cancello, E.M. 1986. Revisão de *Procornitermes* Emerson (Isoptera, Termitidae, Nasutitermitinae). Papéis Avulsos de Zoologia (São Paulo) 36(19): 189-236.

Cancello, E.M. 1989. Revisão de *Cornitermes* Wasmann (Isoptera, Termitidae, Nasutitermitinae). 151p. Universidade de São Paulo, Brasil: Unpublished doctoral dissertation.

Coles, H.R. 1980. Defensive strategies in the ecology of neotropical termites. 243p. University of Southampton: Unpublished doctoral dissertation.

Constantino, R. 1991. Termites (Insecta, Isoptera) from the lower Japurá River, Amazonas State, Brazil. Boletim do Museu Paraense Emílio Goeldi (Série Zoologia) 7: 189-224.

Cruz, B.P.B.; M.B. Figueiredo & E. Almeida. 1962. Principais doenças e pragas do amendoim no Estado de São Paulo. O Biológico (São Paulo) 28: 189-195.

Darlington, J.P.E.C. 1993. Underground foraging passages and storage pits built by the termite *Syntermes molestus* in Goiania, Brazil (Isoptera: Termitidae). Sociobiology 23: 211-212.

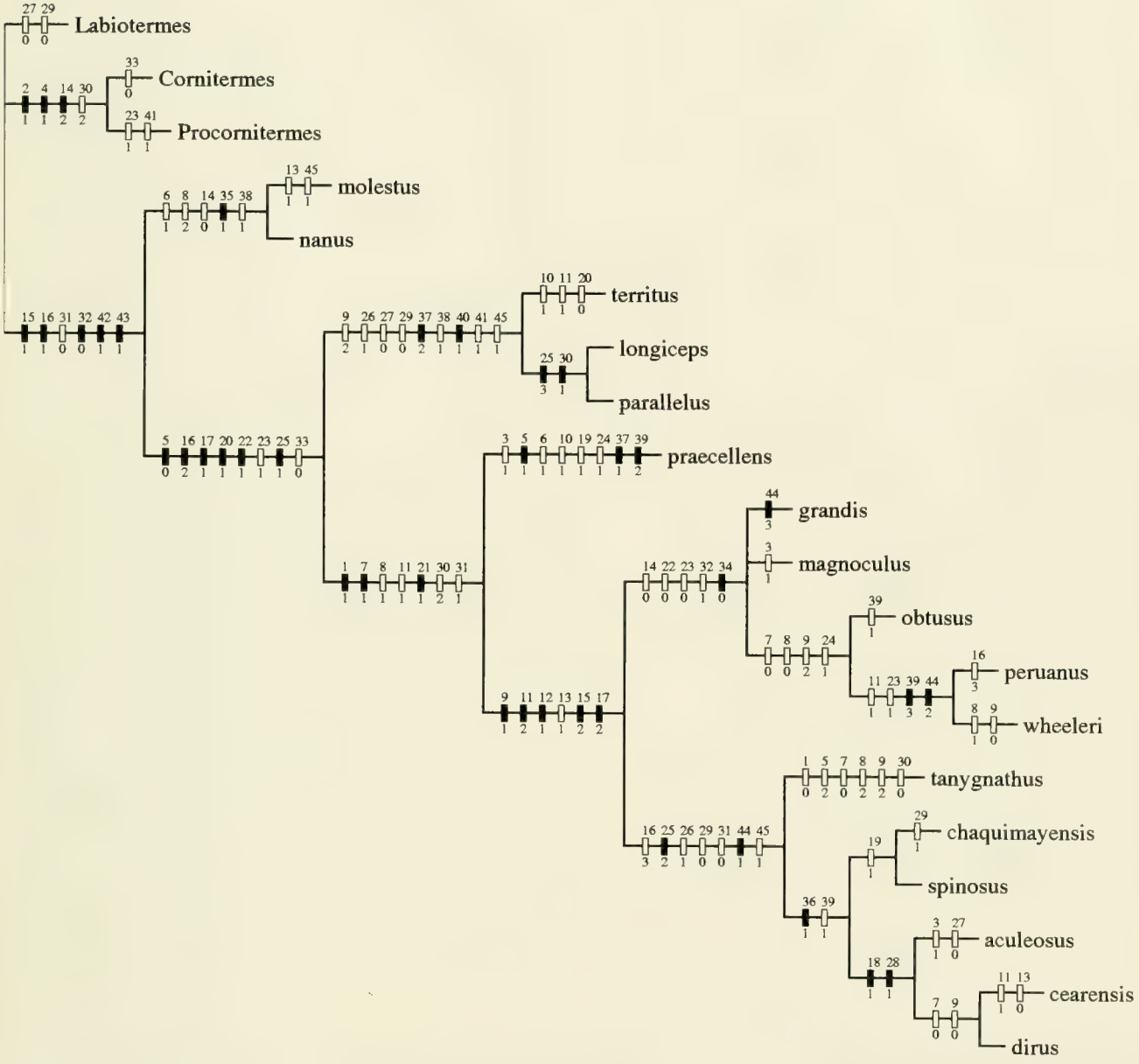


Fig. 331. Tree from analyses 2B (successive weighting) and 2C (implied weights), which both selected the same tree. Only species with known imagoes included. Tree from 2B with length 450, ci= 78, and ri= 91. Tree from 2C with fit= 355.2. Symbols for characters and their states as in Fig. 326.

Desneux, J. 1904. Isoptera, family Termitidae. In: Wytsman, P. (ed.), Genera Insectorum. Pp. 1-52. Bruxelles:

Dufour, D. 1987. Insects as food: a case study from the northwest Amazon. American Anthropologist 89: 383-397.

Dybas, H.S. 1955. New feather-wing beetles from termite nests in the American tropics (Coleoptera: Ptiliidae). Fieldiana: Zoology 37: 561-577.

Emerson, A.E. 1925. The termites from Kartabo, Bartica District, Guyana. Zoologica 6: 291-459.

Emerson, A.E. 1938. Termite nests - a study of the phylogeny of behavior. Ecological Monographs 8: 247-284.

Emerson, A.E. 1945. The neotropical genus *Syntermes* (Isoptera: Termitidae). Bulletin of the American Museum of Natural History 83: 427-472.

Emerson, A.E. 1952. The neotropical genera *Procornitermes* and *Cornitermes* (Isoptera, Termitidae). Bulletin of the American Museum of Natural History 99: 475-540.

Emerson, A.E. & F.A. Banks. 1965. The neotropical genus *Labioter-*

mes (Holmgren): its phylogeny, distribution and ecology (Isoptera, Termitidae, Nasutitermitinae). American Museum Novitates 2208: 1-33.
Erichson, W.P. 1848. Fam. Termitides. In: Schomburgk, R. (ed.), Versuch einer Fauna und Flora von British-Guiana. Pp. 582-583. Leipzig: Bd. 3. Weber.
Farris, J.S. 1988. Hennig86: Version 1.5. Distributed by the author.
Fonseca, J.P. 1949. Experiências de combate químico a cupins subterrâneos no Horto Floresta de Guaraní. Arquivos do Instituto Biológico 19: 57-88.
Fontes, L.R. 1987. Morphology of the alate and worker mandibles of the soil-feeding nasute termites (Isoptera, Termitidae, Nasutitermitinae) from the Neotropical region. Revista Brasileira de Zoologia 3: 503-531.
Goloboff, P.A. 1993. Estimating character weights during tree search. Cladistics 9: 83-91.
Goloboff, P.A. 1994. Pee-Wee: Version 2.1. Distributed by the author.
Guagliumi, P. 1971. Entomofauna della canna da zuchero nel nord-est del Brasile. Rivista di Agricoltura Subtropicale e Tropicale 65: 49-66.
Hagen, H.A. 1858. Specielle Monographie der Termiten. Linnea Entomologica 12: 4-342.
Holmgren, N. 1906. Studien über südamerikanische Termiten. Zoologische Jahrbücher, Abt. Systematik 23: 521-676.
Holmgren, N. 1910. Das System der Termiten. Zoologischer Anzeiger 35: 284-286.
Holmgren, N. 1911. Bemerkungen über einige Termiten-Arten. Zoologischer Anzeiger 37: 545-553.
Holmgren, N. 1912. Termitenstudien 3. Systematic der Termiten. Die Familie Metatermitidae. Kungliga Svesnka Vetenskapsakademiens Handlingar 48: 1-166.
Krishna, K. 1968. Phylogeny and generic reclassification of the termites of the *Capritermes* complex (Isoptera, Termitidae, Termitinae). Bulletin of the American Museum of Natural History 138: 265-323.
Latreille, P.A. 1804. Nouveau Dictionnaire d'Histoire Naturelle. Tome 22. Pp. 49-63. Paris: Deterville.
Luizão, F.J. & H.O.R. Schubart. 1987. Litter production and decomposition in a terra-firme forest of Central Amazonia. Experientia 43: 259-265.
Mariconi, F.A.M.; J.F. Franco; R. Bleicher & N.L. Domiciano. 1976. Combate aos ninhos do cupim *Syntermes* sp. com inseticidas. Anais da Sociedade Entomologica do Brasil 5:200-204.
Mathews, A.G.A. 1977. Studies on Termites from the Mato Grosso State, Brazil. 267p. Rio de Janeiro: Academia Brasileira de Ciências.
Mendonça Filho, A.F. 1972. Insetos observados nos canaviais do estado de Alagoas - Brasil, durante o ano de 1971. Anais da Sociedade Entomologica do Brasil 1: 25-41.
Mill, A.E. 1984a. Predation by the Ponerine ant *Pachycondyla comutata* on termite of the genus *Syntermes* in Amazonian rain forest. Journal of Natural History 18: 405-410.
Mill, A.E. 1984b. Termitarium cohabitation in Amazonia. In: Chadwick, A.C. and S.L. Suton (eds.), Tropical Rain Forest: The Leeds Symposium. Pp. 129-137. Leeds: Leeds Philosophical and Literary Society.
Negret, H.R.C. & K. Redford. 1982. The biology of nine termite species (Isoptera: Termitidae) from the cerrado of Central Brazil. Psyche 89: 81-106.
Nixon, K.C. 1992. Clados: Version 1.2. Distributed by the author.
Noirot, C. 1969. Formation of castes in the higher termites. In: Krishna, K. and F. Weesner (eds.), Biology of Termites. Pp. 311-350. New York: Academic Press.
Noirot, C. 1970. The nests of termites. In: Krishna, K. and F. Weesner (eds.), Biology of Termites. Vol. II. Pp. 73-125. New York: Academic Press.
Noirot, C. and C. Noirot-Timothée. 1969. The digestive system. In: Krishna, K. and F. Weesner (eds.), Biology of Termites. Pp. 49-88. New York: Academic Press.
Ramalho, F.S. 1976. Primeira relação dos insetos que vivem nas plantas cultivadas no brejo paraibano. Anais da Sociedade Entomologica do Brasil 5: 246-257.
Rambur, M.P. 1842. Histoire Naturelle des Insectes, Névroptères. Pp. 300-309. Paris: Roret.
Reichensperger, A. 1936. Beitrag zur Kenntnis der Myrmecophilen- und Termitophilenfauna Brasiliens und Costa Ricas. IV. Revista de Entomologia 6: 222-231.
Roonwal, M.L. 1970. Measurement of termites (Isoptera) for taxonomic purposes. Journal of the Zoological Society of India 21: 9-66.
Seevers, C.H. 1941. New termitophilous Diptera from the Neotropics. Fieldiana: Zoology 24: 175-193.
Seevers, C.H. 1957. A monograph on the termitophilous Staphylinidae. Fieldiana: Zoology 40: 1-334.
Silvestri, F. 1903. Contribuzione alla conoscenza dei Termiti e Termitofili dell'America Meridionale. Redia 1: 1-234.
Silvestri, F. 1923. Descriptiones termitum in Anglorum Guiana. Zoologica 3: 307-321.
Silvestri, F. 1945a. Descrizione di intercaste di *Syntermes grandis* (Rambur) causate da un protozoo microsporidio. Acta Pontificia Academia Scientiarum 9: 77-89.
Silvestri, F. 1945b. Primo contributo alla conoscenza dei termitofili viventi con specie di *Syntermes*. Commentationes Pontificia Academia Scientiarum 9: 515-559.
Silvestri, F. 1946. Nuovo concetto di fasi corrispondenti all'eta della colonia negli individui di una stessa specie componenti una colonia di termiti e descrizione di due specie nuove di *Syntermes*. Bollettino del Laboratorio di Entomologia Agraria (Portici) 6: 1-14.
Snyder, T.E. 1924. Descriptions of new species and hitherto unknown castes of termites from America and Hawaii. Proceedings of the United States National Museum 64: 1-45.
Snyder, T.E. 1948. Our enemy the termite. Ithaca, NY: Cornell University Press, 2nd ed.
Veiga, A.F. 1974. Contribuição ao conhecimento das pragas do cará da costa (*Dioscorea cayenensis* Lam.) e seu controle no estado de Pernambuco. Boletim Técnico Instituto de Pesquisas Agronômicas 69: 1-38.
Wasmann, E. 1894. Kritisches Verzeichniss der myrmecophilen und termitophilen Arthropoden (mit Angabe der Lebensweise und mit Beschreibung neuer Arten). 231p. Berlin: Verlag von Felix L. Dames.
Weesner, F.M. 1969. External anatomy. Pp. 19-43 in: Krishna, K. and F. Weesner (eds.), Biology of termites. New York: Academic Press.
Weidner, H. 1980. Termiten aus Kolumbien nach Beobachtungen von German O. Valenzuela und Fritz Schremmer. Anzeiger für Schädlingskunde Pflanzenschutz Umweltschutz 53: 65-69.
Wheeler, W.M. 1922. Neotropical ants of the genera *Carebara*, *Tranopelta* and *Tranopeltoides*, new genus. American Museum Novitates 48: 1-14.
Wheeler, W.M. 1936. Ecological relations of ponerine and other ants to termites. Proceedings of the American Academy of Arts and Sciences 71: 159-243.

MCZ
LIBRARY
APR 10 1996
HARVARD
UNIVERSITY

THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. 55, No. 14, pp. 519-547 March 4, 1996

Descriptions and Distributional Records of American Mecoptera. IV. [1]

GEORGE W. BYERS

TABLE OF CONTENTS

Abstract 519
Introduction 520
Acknowledgments 520
Panorpa capillata 520
The *Panorpa involuta* species group 522
(*Panorpa involuta*, 522; *contorta*, 523; *ramosa*, 526; *attenuata*, 528; *reclusa*, 530; *mucronata*, 530; key to species, 532)
Panorpa bimacula 532
Panorpa serta 533
Panorpa terminata 535
Bittacus disternum 535
Bittacus sylvaticus 537
Bittacus spatulatus 538
Bittacus peninsularis 540
Bittacus pignatellii 541
Bittacus maculosus 542
Kalobittacus maniculatus 542
Kalobittacus inornatus 543
Kalobittacus demissus 545
Geographic distribution 545
Literature Cited 547

ABSTRACT

Sixteen new species are described and illustrated. These are *Panorpa capillata* (southeastern U.S.A.); *P. involuta* (Veracruz), *P. contorta* (San Luis Potosí and Hidalgo), *P. ramosa*, *P. mucronata* and *P. reclusa* (Hidalgo), *P. attenuata* (San Luis Potosí), *P. bimacula* (Oaxaca), *P. serta* (Michoacán), *Bittacus sylvaticus* (Veracruz) and *B. peninsularis* (Baja California Sur) from Mexico; *Kalobittacus maniculatus* (Guatemala), *K. demissus*, *K. inornatus* and *Bittacus disternum* (Costa Rica), and *Bittacus spatulatus* (Costa Rica and Nicaragua). A lectotype is designated for *Panorpa terminata* Klug, and the male is illustrated. First known males of *Bittacus pignatellii* Navás, from Panama, and *Bittacus maculosus* Byers, from Trinidad, are illustrated and briefly described. Some new distributional data for various species are provided.

[1] Contribution number 3176 from the Snow Entomological Museum and Department of Entomology, University of Kansas, Lawrence, Kansas 66045-2119.

INTRODUCTION

Students and faculty associated with the Snow Entomological Museum at the University of Kansas have in recent years done extensive collecting of insects in Mexico and Central America. Some results of this collecting include new species of Mecoptera described here, as well as new information about the geographic occurrence of other species. Additional new species and distributional data are based on collections received for identification from other sources.

Descriptions of wing venation follow the widely used Comstock-Needham system. Particularly with reference to the Bittacidae, in the taxonomy of which wing venation has long been utilized, some additional abbreviations have been used by Esben-Petersen, others by me. These are: FM - first fork or branching of the media; FRs - first fork of the radial sector; OM - origin of the media from Cu_1 (applies here to Bittacidae only); ORs - origin of the radial sector from R (or R_1); Scv - subcostal cross-vein, from Sc to R_1.

No keys are included for most of the several Mexican or Central American species described here because so many remain to be described that a key could be misleading; however, a tentative key to the *Panorpa involuta* species group in Mexico is included.

ACKNOWLEDGMENTS

For the loan specimens, I am indebted to the following entomologists whose collections are indicated hereinafter by the initials in parentheses:

Mr. Wes Bicha - private collection in Oliver Springs, Tennessee (WB).
Dr. David K. Faulkner - Natural History Museum, Balboa Park, San Diego, California (SDM).
Dr. Eric M. Fisher - California Department of Agriculture, Sacramento, California (CDA).
Dr. Oliver S. Flint, Jr. - Smithsonian Institution, National Museum of Natural History, Washington, D.C. (USNM).
Dr. David G. Furth - Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (now at the USNM) (MCZ).
Dr. Wilford J. Hanson - Department of Biology, Utah State University, Logan, Utah (USU).
Dr. Jean-Michel Maes - Museo Entomológico, SEA, A.P. 527, León, Nicaragua (MELN).
Dr. Mark F. O'Brien - Museum of Zoology, University of Michigan, Ann Arbor, Michigan (UMMZ).
Dr. Edward G. Riley - Department of Entomology, Texas A and M University, College Station, Texas (TAM).
Dr. Roy R. Snelling - Natural History Museum of Los Angeles County, Los Angeles, California (LACM).
The Snow Entomological Museum is abbreviated SEM.

I particularly thank my colleague Wes Bicha for making so many specimens and collection records available for my use and for his helpful comments on this paper.

Two species of *Bittacus* described here (*B. distenuum* and *B. spatulatus*) were included, in 1985, in an unpublished master's thesis by Mr. Ricardo Roggero, then a student at the University of Kansas. I had illustrated and tentatively named them, and he described them, which I acknowledge with thanks. The descriptions here, however, are not his and are based on many additional specimens collected in more recent years.

I wish to thank Sharon Hopkins and Judy Wiglesworth for their patience in entering the paper into computer from my typed and revised copy.

Panorpa capillata new species

Description based on 37 males, 13 females pinned, and 5 males, 5 females in alcohol.

Head: Dorsum unevenly yellowish brown except piceus around ocelli; rostrum yellowish brown to amber brown (probably postmortem color change), terminal segment of maxillary palps apically to wholly brown. Antennal scape yellowish brown, pedicel darker, flagellum dark brown, with 33 to 37 flagellomeres.

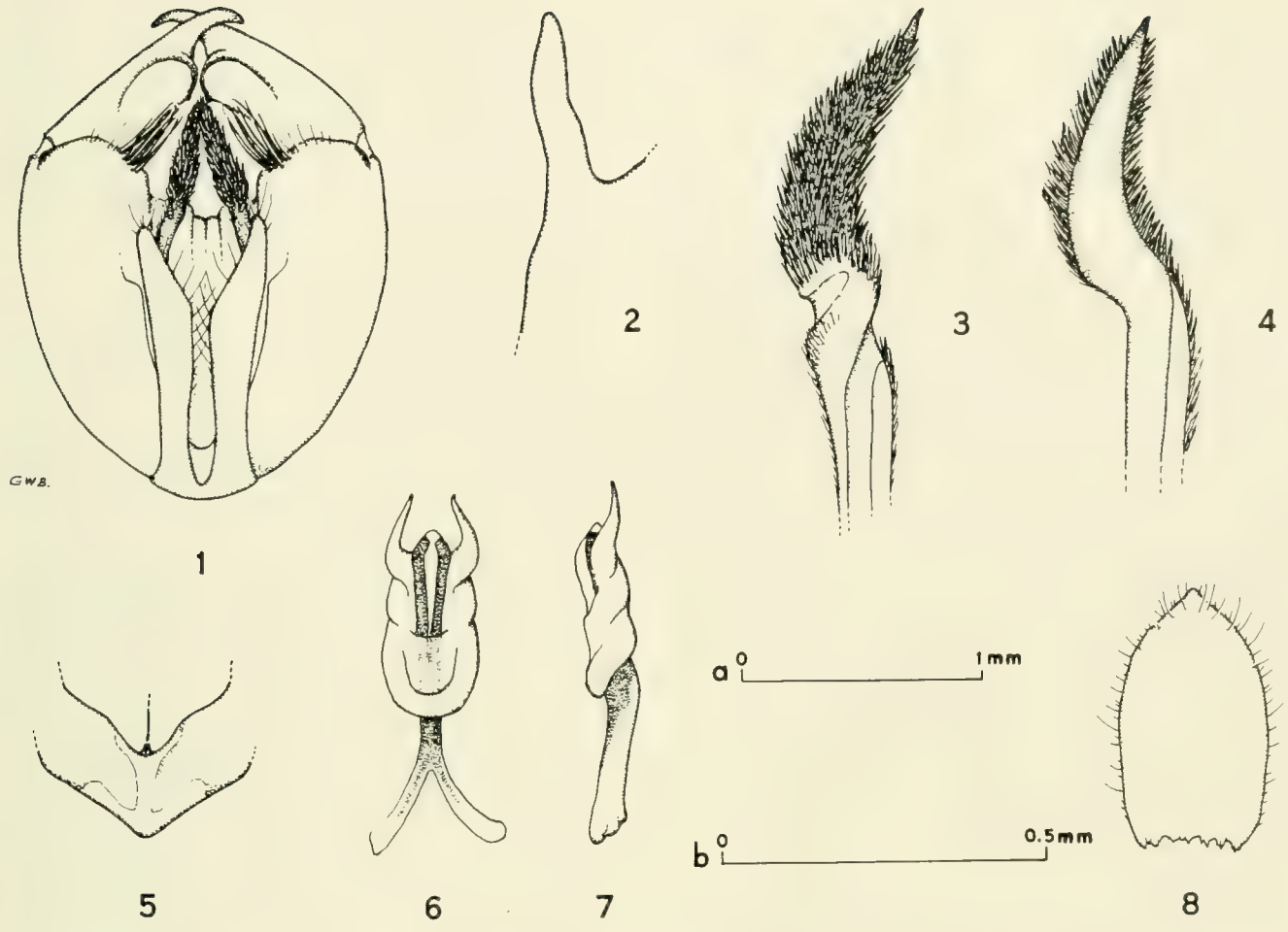
Thorax: Pronotum dull yellowish gray, transversely rugose, with 8 black setae along anterior margin and 2 near posterior margin. Mesonotum yellowish gray with diffuse gray-brown spot at base of each forewing and at anterior edge on each side, spots connected in some individuals. Metanotum sordid yellowish brown to yellowish gray. Pleural surfaces, coxae and mera unevenly amber brown with short, sparse pale hairs, most evident on anterior surfaces of coxae. Femora, tibiae and tarsi pale yellowish brown; conspicuous black setae on tibiae and tarsi.

Wings tinged with pale yellowish brown, sparsely spotted with gravish brown. No complete bands; most cross-veins in distal two-thirds of wing darkly margined; outer radial cells darkened near wing margin in some individuals, especially females. Pterostigmal spot larger than others. First and second basal spots present; humeral spots absent.

Abdomen of male: Unevenly sordid yellowish brown throughout, with short, pale pubescence. No posterior horn on sixth segment. Notal organ a slightly extended, broadly rounded caudal margin on tergum 3, with long, down-curved setae, and a median, setose process on anterior tergum 4. Hypovalves of sternum 9 (Fig. 1) widened beyond mid-length, then narrowed toward apex, with pale yellowish setae along mesal margins except those near apex thickened and darkened to brown in some males. Tergum 9 bilobed, with subrectangular space between lobes. Inner, apical (postero-ventral) margin of each basistyle bearing group of 6-9 black setae of varying thickness, their acuminate tips extending into basal cup of respective dististyle. Outer margins of dististyles (ventral aspect) nearly straight, except apical portion strongly curved and darkly sclerotized; basal cup shallowly concave, ventro-mesal in position, with strongly sclerotized, amber-colored border complete except basally. Ventral parameres (Fig. 3) twisted and transversely grooved near mid-length, with dark amber "barbs" (stout setae) covering ventral and most of lateral surface of apical half of each, except for glabrous, acute apex; marginal barbs of basal half pale, short. Dorsal parameres (Fig. 2) yellowish, dorso-ventrally flattened, blade-like, short, usually concealed by ventral parameres in ventral aspect. Ventral and dorsal valves of aedeagus short, concealed in ventral aspect. Base of aedeagus without distinct hamulus (Byers, 1993: 59), lateral walls of projection forming cup-like structure concave caudally (Fig. 5).

Abdomen of female: Terga 2-6 dark yellowish brown to brown, more terminal segments unevenly yellowish brown; corresponding sterna paler, yellowish brown. Subgenital plate of sternum 8 (Fig.8) mostly flattened ventrally, lateral margins curved upward, apex narrowly rounded, pale (slightly projecting in a female from Rainsville, Alabama, Fig. 8), major marginal setae sparse along sides, more numerous (several submarginal) near apex. Genital plates (Figs. 6, 7) with prolongations of apical plate slender, acute, bowed outward; basal plate roughly U-shaped; axial portion compressed (deeper than wide), extending beyond postero-median margin of apical plate; anterior apodemes slender in ventral aspect, strongly divergent.

Measurements: Body length (based on pinned specimens), male, 9.8-11.3 mm. (holotype 10.4 mm.); female, 10.0-11.2 mm. (allotype 10.0 mm.). Length of front wing, male, 9.2-12.0 mm. (holotype 11.0 mm.); female, 9.9-13.1 mm. (allotype 12.1 mm.). Antennal length, male holotype, about 7.3 mm.; female allotype about 7.4 mm.



Figs. 1-3, 5-8. *Panorpa capillata* n. sp. 1, genital bulb, male holotype, ventral aspect (most hairs omitted). 2, right dorsal paramere, male paratype, ventral aspect. 3, left ventral paramere of male, ventral aspect. **Fig. 4,** left ventral paramere, topotypic male of *Panorpa sigmoides* Carpenter, ventral aspect. 5, lower portion of aedeagus of male, ventral aspect. 6, genital plates of female paratype, ventral aspect. 7, same, right lateral aspect. 8, subgenital plate of female. Scale a, figs. 1, 6-8; scale b, figs. 2-5.

Types: Holotype, male, and 1 male paratype, 10 mi. (16 km) north of Fayette, Fayette Co. (GWB field catalogue no. 1), Alabama, 24 May 1978, G. W. Byers and C. W. Young. Allotype, female, 6 male and 3 female paratypes, Tombigbee State Park southeast of Tupelo, Lee Co. (no. 2), Mississippi, 24 May 1978, G. W. Byers and C. W. Young. Additional paratypes: ALABAMA: Bibb Co., 6 May 1990, Wes Bicha (5 males; WB); Choctaw Co., 0.5 mi. W. of Butler, 23 April 1994, Wes Bicha (2 males; WB); Choctaw Co., 11 April 1982, Wes Bicha (2 males, 1 female; SEM); DeKalb Co., DeSoto State Park, 20 May 1993, G. W. Byers (3 males; SEM); same but 19-23 May 1990, T. Schiefer (1 male; SEM); same but 18-24 May, R. Brown & D. Pollock (1 male; SEM); DeKalb Co., 3.2 km N of Rainsville, 3 June 1975, G. W. Byers (4 females; SEM); Madison Co., Monte Sano State Park, 12 May 1988, D. W. Brzoska (2 males, 2 females; SEM); Marion Co., 30 May 1982, Wes Bicha (1 male; WB); Winston Co. (no. 2), 8.9 km NE of Double Springs, 19 May 1993, G. W. Byers (1 male; SEM). ARKANSAS: Montgomery Co. (no. 1), 14.4 km N of Pencil Bluff, 21 May 1978, G. W. Byers and C. W. Young (2 females; SEM); Montgomery Co. (no. 2), Gap Creek, 2.1 km SE of Joplin, Ouachita National Forest, 22 May 1978, G. W. Byers and C. W. Young (1 male; SEM); Polk Co., Rich Mountain, pitfall trap, 6 July - 10 Nov. 1995, H. W. Robison (2 males; SEM). KENTUCKY: Livingston Co., 31 May 1982, Wes Bicha (2 males, 2 females; SEM); Trigg Co., 8 May 1982 (2 males; WB) and 31 May 1982, Wes Bicha (4 males; WB, SEM). MISSISSIPPI: Lafayette Co. (no. 1), Puskus Lake, 12.8 km NE of Oxford, 23 May 1978, G. W. Byers and C. W. Young (4 males, 3 females; SEM); Lee Co., Tombigbee State Park, 18 May 1993, G. W. Byers (4 males; SEM); 5 May 1982 (1 male) and 30 May 1982, Wes Bicha (5 males; WB, SEM) TENNESSEE: McMinn Co., 20 May 1986, Wes Bicha (1 male; WB). Holotype, allotype and most paratypes in the SEM; 1 male, 1 female paratypes in the USNM; 9 males in collection of WB.

The type locality is a Forestry Research Station of Auburn University, on U. S. Highway 43. *Panorpa capillata* was collected from honeysuckle *(Lonicera)*, with brambles *(Rubus)*, various composites and poison ivy in the same habitat, all shaded by an almost pure stand of tulip trees (or yellow poplar, *Liriodendron tulipifera*), planted in 1953. The understory is typical habitat for this species, usually found in ecotones between woodlands and open fields. At other places where *P. capillata* was collected, the habitat was honeysuckle, brambles, poison ivy, in some places greenbriar and always various broad-leaved herbaceous plants, but the

trees providing shade were of many species. Wes Bicha has found *capillata* (and its more northern counterpart, *P. sigmoides*) also in deep shade along small streams. *P. capillata* is often found together with the similar and probably closely related *P. nebulosa* Westwood.

For some time, I had tentatively identified this species as an aberrant form of *Panorpa sigmoides* Carpenter; but it became apparent that *sigmoides* has a more northern range (Indiana, Illinois, Ohio, Wisconsin, Minnesota), while all specimens of the *capillata* form are from the southern states. It will be interesting to see what future collecting in Kentucky and Tennessee will reveal about the relationships of these two forms.

Panorpa capillata belongs to the *nebulosa* group of species (Carpenter, 1931: 221) and in many details of both males and females resembles *sigmoides* and *nebulosa*. Males of *capillata* may be easily differentiated from both by the ventral parameres (Figs. 1, 3). These are slender and largely bare but have short barbs along the inner edge, in *nebulosa*. The apical one-third of each ventral paramere is expanded, then narrowed to an acute tip, in *sigmoides* and *capillata*, and the barbs are longer. In *capillata* the ventral aspect of a ventral paramere (Fig. 3) shows the apical portion of the paramere covered by dense, slender, recumbent barbs, except on the extreme tip. It is the hairy appearance of the ventral parameres that gives the species its name (Latin *capillata* = hairy). On the dorsal surface, there is a glabrous zone approximately one-third the width of the paramere. The same structure in *sigmoides* (Fig. 4) is broadly glabrous on the ventral surface, with bordering barbs. In *capillata* most setae along the mesal margins of the hypovalves of the ninth sternum are slender and yellowish, but in *sigmoides* they are dark brown to black. And in *capillata* the apical, ventro-mesal setae of the basistyles are thick and black; these are rarely thick or dark in *sigmoides*.

In comparing *capillata* and *sigmoides*, it should be noted that there are some errors in the original description of the latter (Carpenter, 1931: 250-251, fig. 37). The hypovalves are not particularly long and do not reach the ends of the basistyles; neither is the genital bulb elongate and slender. A composite drawing of ventral and antero-ventral aspects of the genital bulb could possibly result in these faulty impressions.

Differentiating females of *capillata* from those of *sigmoides* and *nebulosa* is difficult. In general, there are four spots along the posterior margin of the forewing, in *capillata;* these are (1) a remnant of the proximal edge of an apical band, (2 and 3) in the positions of the branches of the pterostigmal band, and (4) the second basal spot (actually near but not on the margin). These markings are larger and more densely pigmented in *sigmoides* and *capillata* than in *nebulosa*. The genital plates of *capillata* are more slender in ventral aspect than those of *nebulosa* and less slender than those of *sigmoides* (compare my figure 6 with figures 65 and 66 in Carpenter's 1931 revision).

An interesting circumstance, possibly of biogeographical significance, is that there exists in Japan a pair of species having much the same morphology of the male's genital bulb as in *capillata* and *sigmoides*. Particularly with regard to the ventral parameres and the apical setae on the basistyles, *Panorpa kirisimaensis* Issiki is very like *capillata*, and *P. kamikotiensis* Issiki is very like *sigmoides* (Issiki, 1929: 184-187). These Japanese species occur on the islands of Kyushu and Honshu, respectively. Unlike *capillata* or *sigmoides*, they have a horn-like projection from the sixth abdominal segment in males, complete pterostigmal band on the wings, and other differences.

The *Panorpa involuta* species group

The following six species – *Panorpa involuta, P. contorta, P. ramosa, P. mucronata, P. reclusa* and *P. attenuata* – belong to a group apart from other Mexican species of *Panorpa*. As a group they are found in the eastern mountains of Mexico, from approximately the latitude of Ciudad Mante southward to the vicinity of Orizaba. It seems probable that additional species in this group will be discovered within the 500-kilometer band of mountains indicated. In fact, it is likely that *Panorpa mexicana* Banks (1913), known only from its male holotype from Orizaba, belongs to this *involuta* group of species. All six have, in the male, a very complicated aedeagus unlike that seen in other Mexican Panorpas, hence the name given to the one included species and to the group. And all have when alive a decidedly green color, most noticeable in the pleural region of the abdomen and thorax. Whether this pigment is derived from the diet of the scorpion-flies or has some other source (e.g., metabolic) is at present unknown.

A key to the species of the *involuta* group (and including *P. mexicana*) follows the species descriptions.

Panorpa involuta new species

Description based on 52 males, 40 females, pinned, and 3 males, 17 females in alcohol. Colors based on pinned specimens.

Head: Dorsum unevenly light brown to brown; black around ocelli. Rostrum and frons below ocelli yellowish brown to pale brown except rostrum darker brown at sides (apex of rostrum retains green pigment in many individuals); most mouthparts dark brown to black, maxillary palps basally brown, grading through dark greenish gray to almost black on terminal segment. Scape and pedicel yellowish brown, flagellum dark brown with 35-37 flagellomeres, basal one longer than second and third together.

Thorax: Pronotum brown with elevated portions of lateral transverse folds slightly darker; 5-7 thick, black setae at each side on anterior margin. Mesonotum unevenly brown, palest medially gradually darkening at sides (but without pattern), with numerous small, recumbent black setae longest at sides and on scutellum; 1-3 erect black setae above each wing base. Metanotum brown without markings, with numerous short but no long setae. Pleural surfaces, coxae and mera dark yellowish brown to reddish brown, with scattered pale hairs, longest and most dense on anterior surfaces of coxae. Femora yellowish brown, with grayish tinge in some specimens; tibiae and basitarsi darker, grading into dark reddish brown on distal tarsomeres.

Wings (Fig. 99a) moderately iridescent, lightly tinged with gray, markings brown to pale grayish brown. Apical band from slightly before end of R_2 to slightly behind end of M_3 but pigment diffuse and clear areas included; in males, apical band often reduced to

clouding over outer radial and medial cross-veins and narrow darkening along apical wing margin. Pterostigmal band covering basal half of stigma, extending to M_1 then narrowly connected to more slender continuation of band across first cell M_1 to end of M_4; in some males band interrupted from M_1 to M_2. Narrow transverse spot from M_3 to end of Cu_1, another from R_1 across first fork of Rs to M_1 (may be weak between R_{2+3} and R_{4+5}); wider spot from Cu_1 to Cu_2 about midway between cubital cross-veins; small spot at orgin of Rs, from Sc across R_1 to Rs. Whitish thyridium at first fork of M.

Abdomen of male: Terga 2-5 from evenly medium brown to sordid darker brown, corresponding sterna paler brown; segments 6-9 brown. Notal organ weakly developed: narrow, short projection from posterior margin of tergum 3 with few downcurved, black setae; small, sclerotized, forwardly projecting point on tergum 4. Dorsum of segment 6, in lateral aspect, conspicuously concave in posterior half. Hypovalves (Fig. 9) short but exceeding ventral connection between basistyles, borne on gradually narrowing prolongation of ninth sternum nearly twice length of hypovalves, in ventral aspect. Tergum 9 (Fig. 10) narrowed gradually past level of cerci; apex shallowly emarginate. Basistyles separated less than half their length, in ventral aspect. Inner, postero-ventral margin of each basistyle bearing about 12 mesally directed setae (Fig. 11); other setae on mesal surface of basistyle. Outer margins of dististyles slightly concave before mid-length; basal cup of dististyle elongated ventro-mesally, shallowly concave on lower (anterior) surface; row of long hairs extending from basal cup past mid-length of dististyle; inner margin of dististyle with sharp, strongly sclerotized, downwardly curved point concealed by basal cup in ventral aspect (Fig. 12). Ventral parameres two-branched (Figs. 22, 23), ventral branches elongate, with apices crossing and projecting conspicuously from genital bulb in lateral aspect; dorsal branches elongate, each bearing pendulous, membranous inner appendage. Dorsal parameres elongate, not darkly sclerotized, with two acute, triangular "teeth" on ventro-lateral surface of each and two tiny "teeth" nearer base. Ventral valves slender, dark but not densely sclerotized, evenly curved, tips usually visible between tips of lower branches of ventral parameres; dorsal valves short, blunt, dark and densely sclerotized.

Abdomen of female: Terga 2-4 or 2-5 unevenly brown, sterna paler; more posterior segments grayish brown, sometimes with faint indication of green. Subgenital plate (Fig. 13) slightly widened behind mid-length, posterior margin broadly rounded with about 20 setae longer than others on plate. Genital plates (Fig. 24) narrow, with only small, nearly transparent lateral extensions representing apical plate, "basal plate" semimembranous and poorly defined, attached to adjacent tissues anteriorly; axial portion strongly sclerotized but anterior ends of slightly divergent apodemes relatively pale. In lateral aspect, structure nearly straight, anterior ends of apodemes curved slightly ventrad.

Measurements: Body length (based on pinned specimens), male, 8.6-11.0 mm (holotype 10.3 mm); female, 8.4-12.0 mm (allotype 10.5 mm). Length of fore wing, male, 10.7-11.6 mm (holotype 11.4 mm); female 11.3-12.8 mm (allotype 12.2 mm). Antennal length, male, about 8.7 mm, female about 8.5 mm.

Types: Holotype, male, collected in cloud forest, 4.8 miles (7.7 km) northeast of Coscomatepec, Veracruz, Mexico, elevation about 1420 m, on 8 August 1969, by G. W. Byers (field cat. Veracruz no. 17). Allotype, female, same data but 9 August (no. 18). Paratypes, 15 males, 13 females, pinned, 3 males, 5 females in alcohol, same data as holotype; 16 males, 11 females, pinned, 12 females in alcohol, same data as allotype; same locality but 23 June 1971, N. D. Penny (5 males, 3 females, SEM); same locality but 31 August 1971, G. W. Byers and R. Thornhill, 8 males, 9 females, SEM; Veracruz, Coscomatepec, km 29, 16 August 1993, Wes Bicha (7 males, 3 females, WB). Holotype, allotype and most paratypes are in the SEM; paratypes have been sent to the USNM, the MCZ, the UMMZ and some other collections.

This species takes its name from the complicated aedeagus of the male (Latin *involuta* = complex, intricate).

At the time I first collected this species, the habitat was cloud forest of numerous kinds of tropical broad-leaved trees, some tree-ferns, shrubs, many vines, ferns, mosses, abundant bromeliads and other epiphytes on tree branches, and a peculiar ground cover of *Selaginella* about 10-15 cm. deep. Returning to the site three years later, I found that while some of the highest trees had been left to provide shade, most of the lower trees and native shrubs had been cut and burned, and coffee shrubs planted in their place. There were extensive areas of bare or nearly bare soil with only patches of *Selaginella* left. Nevertheless, *P. involuta* was still present, especially in streamside leafy, herbaceous vegetation.

When alive, *Panorpa involuta* displays a bright green (less often yellowish green) color, particularly noticeable on the thoracic and abdominal pleura, rostrum and legs but even in some well sclerotized structures, for example, the genital bulb of males. Eventually this color largely disappears from specimens pinned and dried, but it leaches out rapidly from those preserved in alcohol.

Panorpa involuta somewhat resembles *P. mexicana* Banks, a species still known only from its male holotype, collected near Orizaba, Veracruz, only about 35 km from the type locality of *P. involuta.* In the male of *involuta,* the hypovalves extend slightly past the edge of the ventral connection between the basistyles, while in *mexicana* they clearly terminate short of this edge. There are numerous dark, conspicuous setae on the posteroventral surface of the basistyle, in *involuta,* but in *mexicana* there are only more slender, shorter and paler setae. The ninth tergum in *involuta* is shallowly emarginate at apex, while that of *mexicana* appears to be rounded (seen only from the side). There are only two spots proximal to the pterostigmal band in the fore wings of the type of *mexicana* but four in males of *involuta.* I did not examine the aedeagus of *mexicana* in detail, but in ventral aspect (cf. Byers, 1962: 303, fig. 8) it is evidently very different from that of *involuta.*

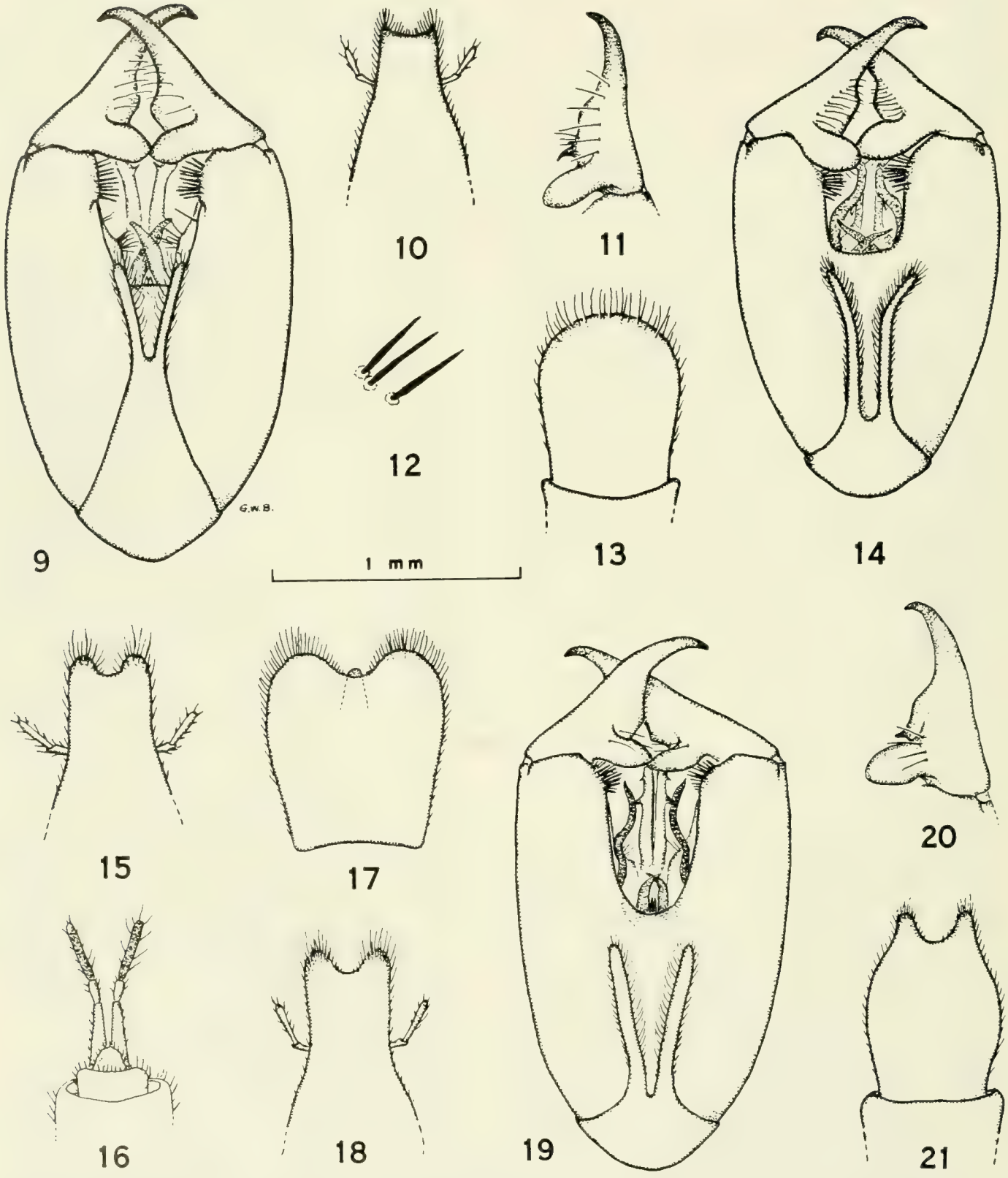
Panorpa contorta new species

Description based on 35 males, 12 females, pinned, 4 males, 1 female in alcohol.

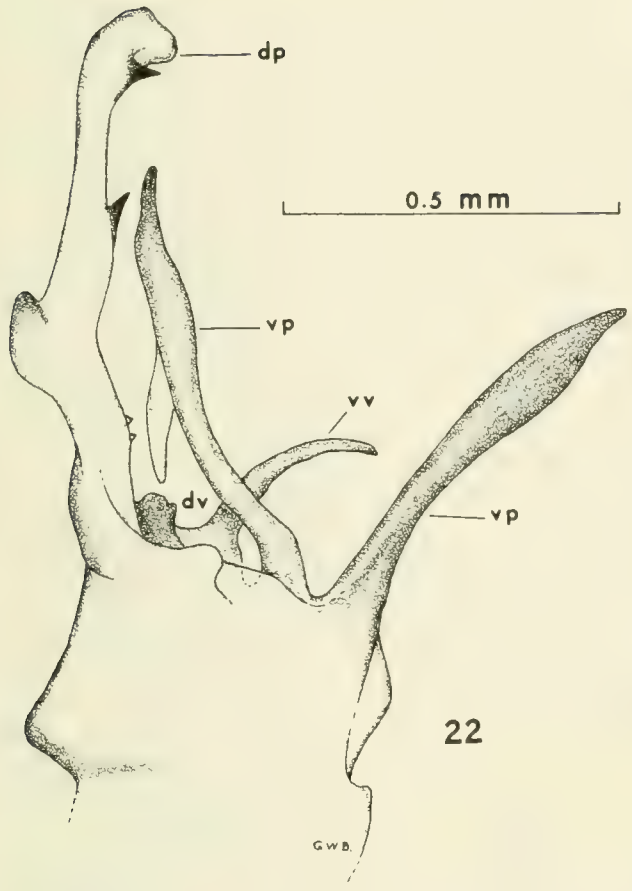
Head: Dorsum yellowish brown, dark brown to black around ocelli. Rostrum and frons below ocelli mostly yellowish brown, rostrum slightly darker at sides, with trace of green near apex and in maxillary palps. Apical half of terminal segment of palps blackish brown. Scape yellowish brown, pedicel brown, flagellum dark brown to black with 33-35 flagellomeres, first subequal in length to second and third together.

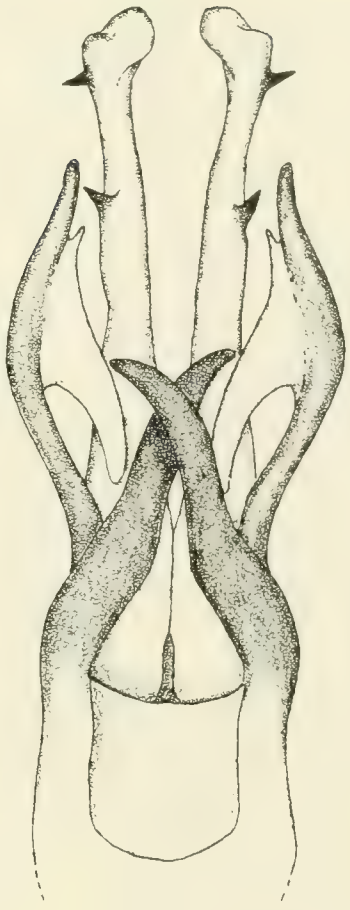
Thorax: Pronotum yellowish brown in depressed areas, slightly darker brown on elevated, transverse ridges or folds; 7-8 black setae on each side of anterior margin. Mesonotum and metanotum unevenly light brown, with short, dark setae directed backward; two longer setae on mesonotal scutellum. Pleural surfaces, coxae and mera unevenly yellowish brown with sparse, pale setae; setae longest and most dense on anterior surfaces of coxae. Femora and tibiae yellowish brown, usually with tinge of green visible in femora; setae black; tarsi light brown.

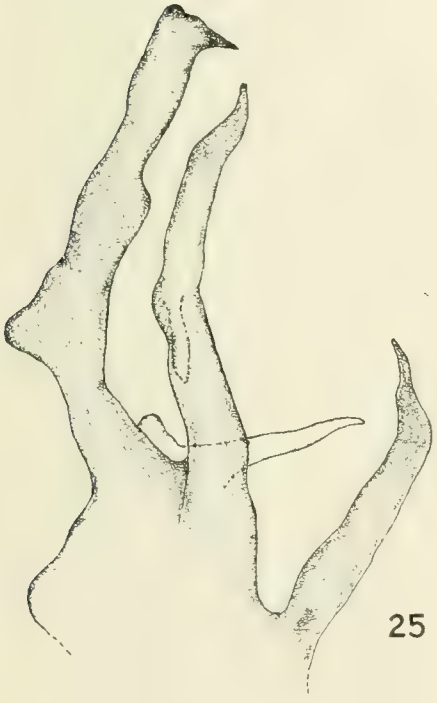
Wings without any complete bands, tinged with yellowish brown, iridescent, with brown stigma and markings. Narrow darkening at edge of wing in outer radial cells; transverse spot across outer radial cells from about R_3 to slightly behind R_5 or to M_1. Pterostig-

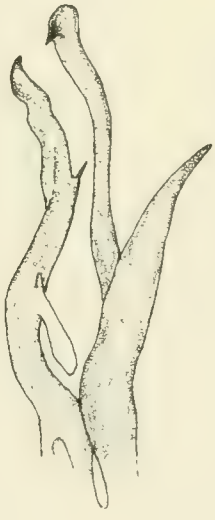


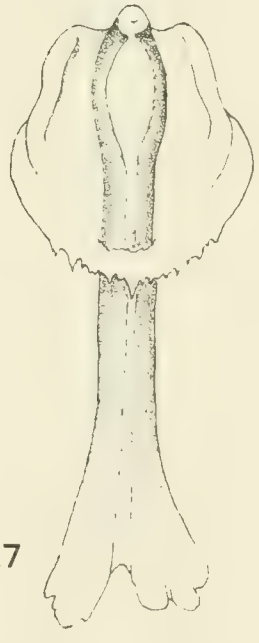
Figs. 9-13. *Panorpa involuta* n. sp. 9, genital bulb, male holotype, ventral aspect (most hairs omitted). 10, ninth abdominal tergum, male paratype, dorsal aspect. 11, right dististyle, male paratype, posteroventral aspect. 12, setae of ventromesal surface of basistyle. 13, subgenital plate, female paratype. **Figs. 14-17.** *Panorpa contorta* n. sp. 14, genital bulb, male paratype, ventral aspect. 15, ninth abdominal tergum, male paratype, dorsal aspect. 16, terminal abdominal segments and cerci, female allotype, ventral aspect. 17, subgenital plate, female allotype, ventral aspect. **Figs. 18-21.** *Panorpa ramosa* n. sp. 18, ninth abdominal tergum, male holotype, dorsal aspect. 19, genital bulb, male holotype, ventral aspect. 20, right dististyle, holotype, posteroventral aspect. 21, subgenital plate, female allotype, ventral aspect. Scale, figs. 9-11, 13-21.











Figs. 22-24. *Panorpa involuta* n. sp. 22, aedeagus, male paratype, left lateral aspect; dp - dorsal paramere, dv - dorsal valve, vp = ventral paramere (both branches labelled), vv - ventral valve. 23, same, ventral aspect. 24, genital plates of female, ventral aspect. **Figs. 25-28.** *Panorpa contorta* n. sp. 25, apex of male aedeagus, left lateral aspect. 26, left half of aedeagus, ventral aspect. 27, genital plates of female, ventral aspect. 28, same, right lateral aspect. Scale, all figures.

mal band represented by wedge-shaped spot from basal half of stigma to outer nygma, slightly behind R_4 (interrupted between R_4 and R_5 or offset near fork of R_{4+5} in some individuals). Small spots in first cell R_1, at origin of radial sector, between 1A and 2A about halfway between cross-veins, and at end of Cu_1. Other spots in some specimens. Hind wings with lighter markings, virtually unmarked in some males. Cross-veins in outer radial-medial area usually not bordered in males, or may be slightly bordered, especially in females, most of which have more wing spots than in males (e.g., from end of Cu_1 to M_3, Cu_1 to Cu_2 at level of ORs, or at ends of 1A and 2A).

Abdomen of male: Terga 2-6 unevenly yellowish brown with short, pale setae; corresponding sterna slightly paler. Notal organ formed of broadly rounded, slight median prolongation of tergum 3 and small peg with sharp tip curved cephalad on anterior tergum 4. Dorsum of posterior half or more of segment 6 depressed, without setae, to accommodate genital bulb when brought fully forward. Hypovalves of ninth sternum (Fig. 14) slender, of nearly uniform width throughout, slightly divergent, extending to or slightly beyond edge of ventral connection between basistyles (may be bent to sides in apical half due to drying), separated at base by width of a hypovalve or more, with yellowish hairs along mesal edges longer and more numerous than those along outer edges. Tergum 9 arched dorsad in basal half, abruptly narrowed at level of cerci, shallowly emarginate and bilobed at apex (Fig. 15). Inner, subapical surface of each basistyle bearing numerous mesally-directed, thick black setae. Outer margins of dististyles slightly concave near mid-length, strongly curved subapically and increasingly sclerotized. Basal cup of dististyle about 1.5 times as long as its greatest width, with pale, curved setae along lower edge, sparse setae on outer curvature. Strongly sclerotized point on mesal margin of dististyle concealed by basal cup in ventral aspect. Both branches of ventral parameres thick, well sclerotized (Figs. 25, 26), with small membranous appendage on somewhat twisted dorsal branch. Dorsal parameres with single spinous projection at apex and heel-like swelling on dorsal surface near base. Dorsal valves short, rounded, inconspicuous; ventral valves elongate, not strongly sclerotized.

Abdomen of female: Terga 2-6 unevenly dark yellowish brown to brown; corresponding sterna pale yellowish brown; more terminal segments sordid brown or grayish brown. Basal segment of cercus brown, short (Fig. 16); apical segment black, more than twice length of basal segment; cercal bases unusually deeply separated. Subgenital plate (Fig. 17) broad, apically bilobed with short median projection in most specimens. Genital plates (Figs. 27, 28) with stout axial portion and only distal plate well sclerotized; basal plate largely membranous, its limits indistinct; distal plate curved ventrad at sides. Anterior apodemes thick, moderately divergent.

Measurements: Body length, male, about 9.3-11.6 mm (holotype 10.2 mm); female, 9.2-11.0 mm (allotype 9.6 mm). Length of fore wing, male, 10.3-13.0 mm (holotype 10.5 mm); female, 11.5-11.9 mm (allotype 11.6 mm). Antennal length, male, about 8.8 mm, female about 9.9 mm.

Types: Holotype male, allotype female, 4 male and 3 female paratypes collected 14.9 miles (23.8 km) by road west of El Naranjo, San Luis Potosí, Mexico, 26 August 1972, elevation 4000 ft. (1220 m), by G. W. Byers and R. Thornhill (GWB field catalogue no. 15). Additional paratypes: San Luis Potosí, 16 miles west of El Naranjo, 8 September 1992, Wes Bicha (9 males, 3 females); same but 9 Sept. 1992, Wes and Fred Bicha (15 males, 4 females); Tamaulipas, Rancho del Cielo, near Gomez Farias, 3 July 1989, R. Jones (5 males, one without terminal segments); same, about 7 miles (11.2 km) west of Gomez Farias, 6-7 July 1986, Jones and Kovarik (1 male); Hidalgo, 22 miles (35.2 km) by road northeast of Jacala, 5300 ft. (1615 m), 27 August 1972, G. W. Byers and R. Thornhill (1 female; GWB no. 16). The type locality in San Luis Potosí is approximately 14 km northeast of Ciudad del Maíz. El Naranjo does not appear on most maps of Mexico. It is on Highway 80, the road from Antiguo Morelos (on Highway 85, the Interamerican Highway) to Ciudad del Maíz, and is approximately 29 km west of Antiguo Morelos, where a road turns north to Salto de Agua (known locally as El Salto). Holotype, allotype and 4 male, 4 female paratypes in the SEM; 18 males, 2 females in collection of Wes Bicha; 6 male paratypes in collection of TAM.

Panorpa contorta is the only Mexican species known to occur significantly below 5000 feet (approximately 1525 meters), which may relate to the fact that it is also the northernmost *Panorpa* known in Mexico.

At the type locality in San Luis Potosí, the general habitat was an oak forest in fairly high mountains (2.56 km by road southwest of the summit), with abundant epiphytic bromeliads, mosses and liverworts on the larger trees. Undergrowth included woody shrubs up to 2 m high, also low herbaceous plants .6 to 1 m high on which *Panorpa contorta* was found, together with another species of *Panorpa* as yet unnamed. The decidedly greenish *P. contorta* held its wings roof-like above the body, at rest, occasionally raising them in a "fanning" motion.

By its green color in life, its wing maculation, and by the complicated structure of the male aedeagus (Latin *contorta* = intricate, complex, twisted), *P. contorta* shows close similarity to *P. involuta* of Veracruz. It differs from *involuta* and other related species in details of the aedeagus and conformation of the hypovalves, in the male, and the broadly bilobed subgenital plate and characteristic genital plates, in the female.

Panorpa ramosa new species

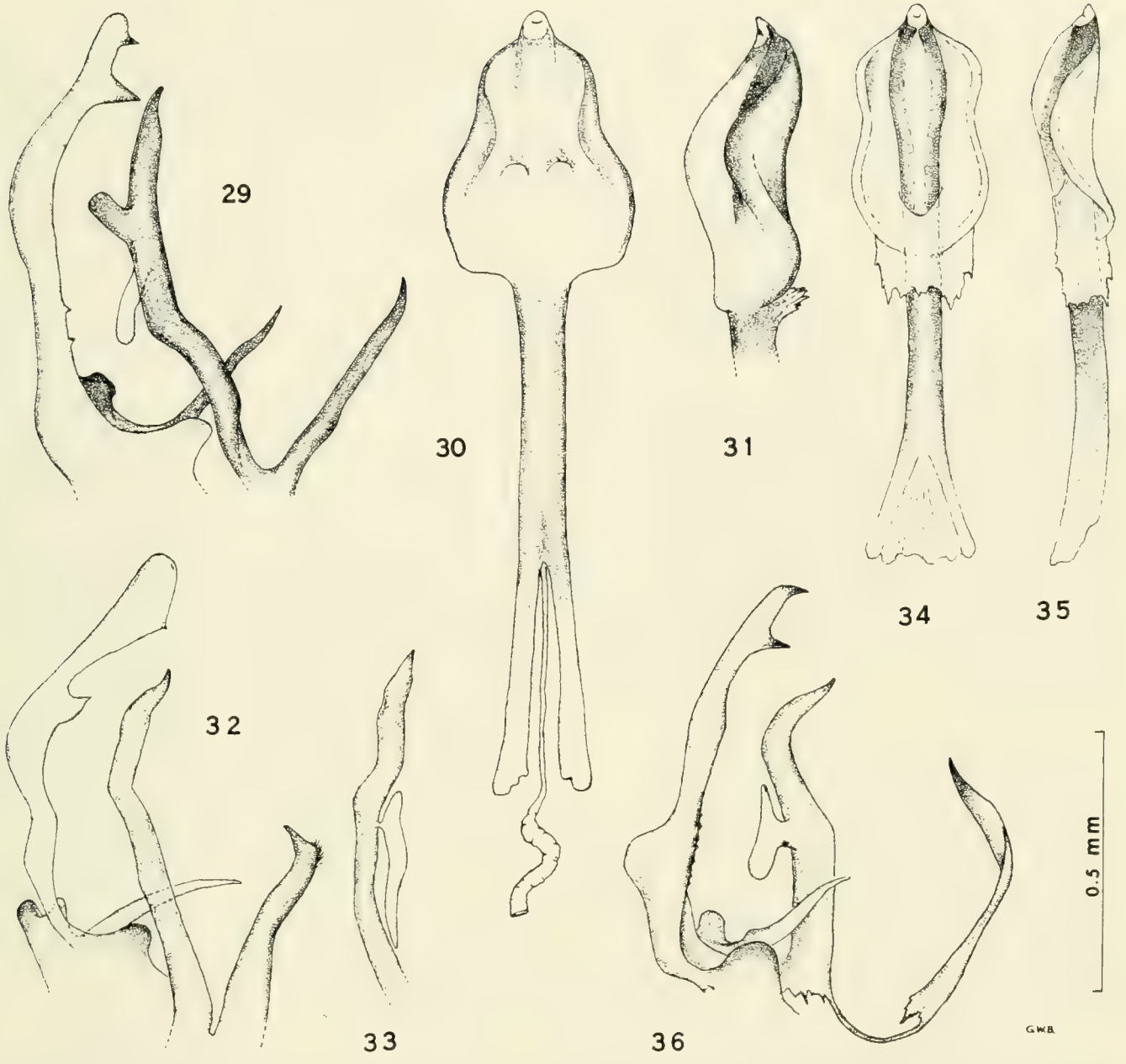
Description based on one male, two females, preserved in alcohol.

Head: Dorsum pale yellowish brown to tan with appressed black hairs; black around ocelli; rostrum pale yellowish brown, unmarked, with numerous erect, black hairs. Mouthparts yellowish brown; apical half of terminal segment of maxillary palp and all of terminal segment of labial palp dark brown. Antennal scape pale tan, pedicel brown, flagellum black with 37 (holotype) or 38 flagellomeres.

Thorax: Pronotum light tan variegated with brown, almost white at lateral edges; six (male) to eight (female) conspicuous black setae and numerous smaller ones at each side along anterior margin; short black setae on posterior margin. Dorsum of cervix light brown in females, gray in male. Mesonotum and metanotum pale tan with irregular light brown shading along each side; numerous recumbent black setae on scutum and scutellum, directed caudad. Pleural surfaces, coxae and mera pale tan with scattered, mostly pale hairs, but hairs darker on anterior surfaces of coxae. Femora and tibiae pale yellowish gray with black setae; tarsi slightly darker, apical tarsomere dark brown to black, setae black; basitarsus nearly as long as tarsomeres 2-5 together.

Wings hyaline, very lightly tinged with gray-brown, iridescent, with dark brown markings; apical spot (or band) approximately from end of R_2 to end of M_1; pterostigmal band roughly triangular, its short base along costa, covering proximal half of stigma, apex at or near M_1; outer half of stigma light brown.

Abdomen of male: Terga 2-5 pale yellowish gray medially, irregularly darker gray at sides; corresponding sterna extremely pale gray, nearly white; pleura white (but see note on color in discussion); segments 6-9 yellowish brown. Notal organ weakly developed, with slight, wide backward extension of tergum 3 bearing downcurved, black setae; small, median elevated point on tergum 4. Genital bulb (Fig. 18) elongate and narrow. Hypovalves short, slender, deeply separated. Tergum 9 narrowed before level of cerci, apically bilobed; lobes broad, rounded, slightly darkened at apex (Fig. 19). Basistyles separated ventrally less than half their length,



Figs. 29-31. *Panorpa ramosa* n. sp. 29, aedeagus of male holotype, left lateral aspect. 30, genital plates, female, ventral aspect. 31, genital plates, female, anterior apodemes omitted, right lateral aspect. **Figs. 32-35.** *Panorpa attenuata* n. sp. 32, aedeagus of male holotype, left lateral aspect. 33, dorsal branch of left ventral paramere, ventral aspect. 34, genital plates, female, ventral aspect. 35, same, right lateral aspect. **Fig. 36.** *Panorpa reclusa* n. sp., aedeagus of male holotpe, ventral parameres (both branches) removed from left or near side. Scale, all figures.

each with group of black setae on inner, postero-ventral margin. Outer margins of dististyles slightly concave before mid-length, strongly curved in distal one-third to darkly sclerotized tips; basal cup of dististyle elongated ventro-mesally, shallowly concave (Figs. 18, 20), with four long, black setae on caudal surface; mesal margin of dististyle bearing acute point normally concealed in ventral aspect. Ventral parameres (Fig. 29) biramous, lower branches curved mesad, their tips crossing; dorsal branches sinuous, acutely tipped, each extending caudad alongside respective dorsal paramere, with bluntly rounded lobe projecting dorsad and nearly transparent, pendulous branch directed basad. Dorsal parameres elongate, paler than ventral parameres, each with two subapical spines, or "teeth", on ventral surface, basal one larger; two tiny ventral spines near base. Ventral valves elongate, slender, darkened toward acuminate tips; dorsal valves short, rounded, darkly sclerotized.

Abdomen of female: Terga yellowish brown to brown, sterna 2-7 pale gray, nearly white. Irregular dark spot from each side of ter-

gum 1 down over pleuron to metathoracic meron. Subgenital plate (Fig. 21) widest near mid-length, bilobed at apex with median emargination broadly U-shaped. Genital plates (Figs. 30, 31) unusually long for genus, axial portion projecting beyond apical plate, sides of basal plate strongly curved in lateral aspect (Fig. 31); anterior apodemes about ten times as long as width of portion posterior to separation, only slightly divergent.

Measurements: Body length, male holotype, about 14.2 mm, female allotype 13.8 mm, female paratype 9.9 mm (but possibly deformed by damage when collected); fore wing, male, 12.7 mm, female 12.7 (allotype) to 12.8 mm. Antennal length, male, about 11.3 mm, female, about 11.6 mm.

Types: Holotype male, allotype female and one female paratype all collected near highway 105, 4.4 km northeast of Tlanchinol (about 98 km NNE of Pachuca), Hidalgo, Mexico, on 6 July 1992, by J. S. Ashe (his collection no. 8). Elevation at this site is 1420 m; the habitat is cloud forest with large tree ferns, dense moses on trees; the scorpion-flies were on low foliage. All three specimens are in the SEM.

Panorpa ramosa is one of several species (most of them previously undescribed) of the highlands of east-central Mexico that when alive are distinctly greenish, that color being particularly evident in the pleural areas of thorax and abdomen. In callow individuals, even sclerotized areas may be greenish, for example, the genital bulb of males, the legs, and less often the head. Dr. Ashe's field notes comment that the "original color of body was a striking lime green" which "faded in alcohol within a few hours." *Panorpa mexicana,* described by Banks (1913) as "pale yellowish," was probably one of these that was greenish prior to being preserved; the only known specimen of it is a male from "Orizaba, Mexico."

Panorpa attenuata new species

Description based on one male, six females, pinned.

Head: Dorsum sordid yellowish brown (holotype) to medium brown; dark brown around ocelli. Rostrum and frons below ocelli dark yellowish brown (holotype) to unevenly brown, rostrum dark amber-brown at sides, palest apically; mouthparts light brown to amber-brown, apical segment of maxillary palps darkened in most individuals (not holotype). Scape and pedicel yellowish brown to brown, flagellum blackish brown to black with 37-38 flagellomeres, basal one nearly equal in length to second and third together.

Thorax: Pronotum dark yellowish brown, darkest on transverse folds; three or four black setae at each side on anterior margin; a few slender setae near posterior margin. Mesonotum and metanotum sordid yellowish brown, without darker markings; numerous short, recumbent setae on scutum, slightly longer at sides; few longer setae on scutellum. Pleural surfaces, coxae and mera unevenly yellowish brown with scattered yellow hairs, longest and most dense on anterior surfaces of coxae. Femora and tibiae yellowish brown, larger tibial setae black; tarsomeres 1-3 yellowish gray, darker than tibiae; tarsomeres 4-5 grading from gray to black near claws; trace of greenish pigment in tarsi of some individuals.

Wings moderately iridescent, lightly tinged with brown, markings brown. Apical band represented by faint, narrow marking across outer radial and medial cells with longitudinal connection in outer R_5 cells; more nearly complete apical band in one female. Pterostigmal band complete but narrow and irregular, from proximal end of stigma to end of M_4 (interrupted between M_1 and M_2 in one female). Transverse spot from M_3 to tip of Cu_1, another from R_1 to nygma between R_{4+5} and M_{1+2}; wider spot from Cu_1 to posterior margin at end of 1A; small spot at FRs. Whitish thyridium at FM.

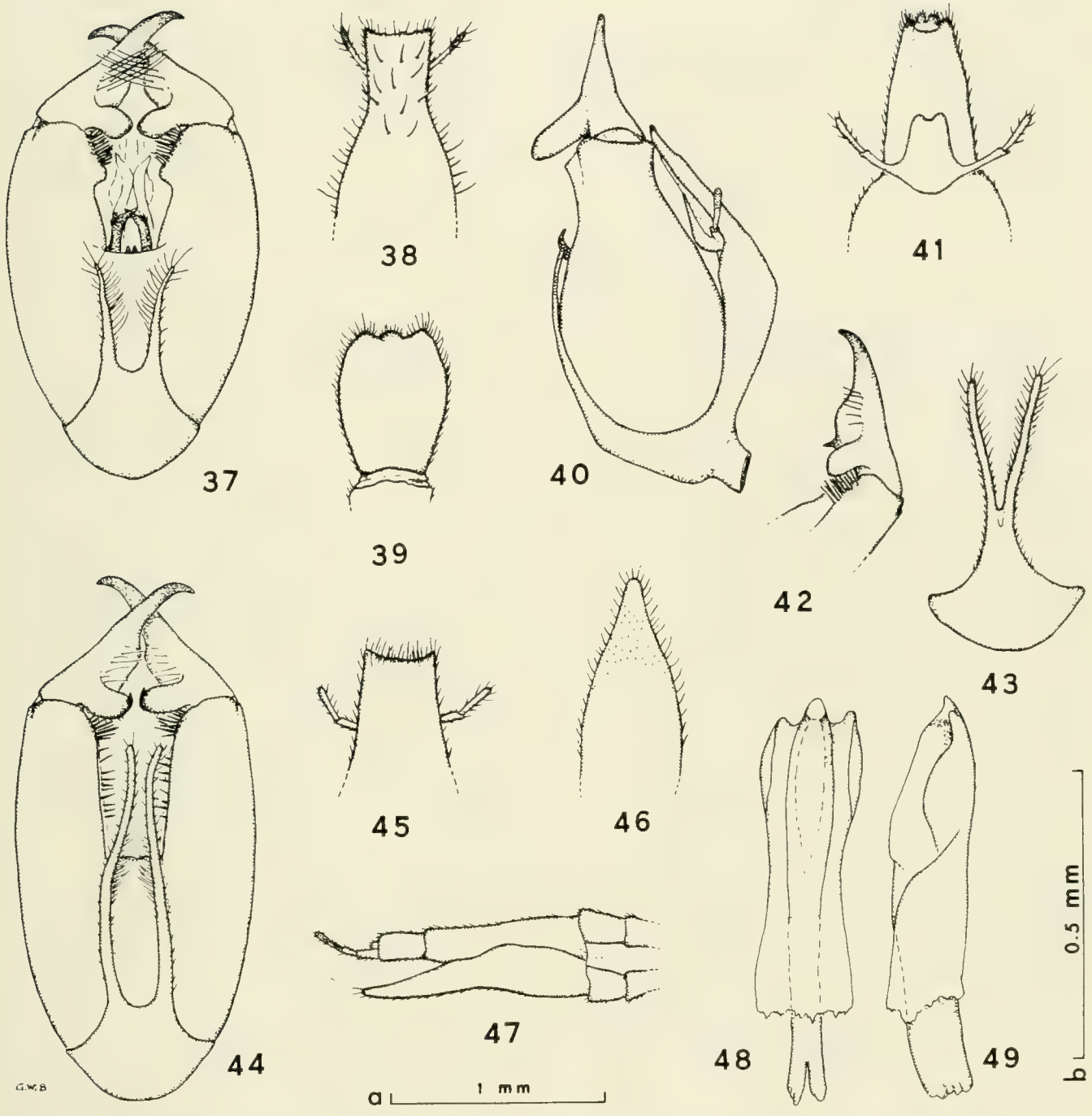
Abdomen of male: Terga 2-5 unevenly yellowish brown, corresponding sterna paler; segments 6-9 yellowish brown. Notal organ a short projection from posterior margin of tergum 3, with rounded apex and numerous downcurved hairs, and triangular peg on tergum 4 with sclerotized apex curved cephalad. Posterior half of dorsum of sixth segment concave in lateral aspect, without setae. Hypovalves (Fig. 37) short, not reaching edge of ventral connection between basistyles, slender and attenuate toward tips, separated basally by more than basal width of a hypovalve. Ninth abdominal tergum (Fig. 38) truncate or very shallowly emarginate at apex, slightly darkened at corners, with sparse dark setae on dorsum, pale, yellowish setae on margins; cerci dark gray at apex. Basistyles separated slightly more than half their length, in ventral aspect (Fig. 37); inner postero-ventral margin of each bearing about 14 thick, black setae directed mesad and beneath these a conspicuous, rounded prominence on mesal surface of basistyle. Dististyles with 6-7 long setae above basal cup (Fig. 37); outer margin slightly concave near mid-length; sharp, sclerotized point on mesal margin, concealed by basal cup in ventral aspect. Ventral parameres (Fig. 32) two-branched, ventral branches acute at apex, with small subapical tuft of short setae, their tips overlapping, projecting slightly from genital bulb; each dorsal branch bearing a pendulous, membranous appendage on mesal surface (Fig. 33). Dorsal parameres elongate, sinuous, flattened and expanded in apical one-third, with small, subapical point and larger, more proximal point on ventral margin (Fig. 32). Ventral valves yellowish (appear darker in ventral aspect), long and slender; dorsal valves dark, with rounded lobe at each side of ventral valves.

Abdomen of female: Terga 2-5 unevenly sordid yellowish brown, corresponding sterna paler in most females; segments 6-9 darker yellowish brown throughout. Subgenital plate widest near mid-length, unusually deep in lateral aspect, with three posterior marginal lobes, center lobe more broadly rounded than lateral ones and somewhat darkened. Genital plates (Figs. 34, 35) comprised of elongate axial portion and laterally rounded apical and basal plates (not distinctly separated); anterior apodemes divergent, but intervening region sclerotized, curved slightly ventrad anteriorly.

Measurements: Body length, male holotype, about 11.6 mm; female, 10.1-10.6 mm (allotype 10.1 mm). Length of fore wing, male, 11.0 mm; female, 11.3-12.6 mm (allotype 11.3 mm). Antennal length, male, about 7.8 mm, female about 10.0 mm.

Types: Holotype, male, allotype and five female paratypes collected beside Highway 85 (Interamerican Highway), 32 km southwest of Tamazunchale (labels say 20 mi. west), San Luis Potosí, Mexico, 19 September 1974, by W. J. Hanson and G. E. Bohart. At the suggestion of Dr. W. J. Hanson, the holotype and allotype are deposited in the SEM, and the paratypes are in the collection of Utah State University, Logan, Utah. It was also Dr. Hanson who clarified the collection site; he found, from his field notes, that he collected both *Panorpa* and *Bittacus* in second-growth forest on the slope above the highway.

Panorpa attenuata superficially resembles its geographically nearest neighbor species, *P. contorta* (from Hidalgo), and in wing markings somewhat resembles other species in the *involuta* species group. In several details, however, it differs from all these. Males of *attenuata* can be recognized readily by the short, attenuate hypovalves (Fig. 37), for which the species is named (Latin *attenuata* = drawn out, thin, tapered). The rounded protuberance on the mesal margin of each basistyle and the unusually long setae on the ventral surface of the dististyles are both unique among known Mexican Panorpas. Dissection reveals the equally unique aedeagus (Fig. 32), unlike that of *P. contorta* but showing affinity with the *involuta* species group. The subgenital plate of females of *P. attenuata* resembles that of *P. contorta* in having the posterior margin somewhat three-lobed; but the plate is widest near its posterior end and has broadly rounded lat-



Figs. 37-39. *Panorpa attenuata* n. sp. 37, genital bulb of male holotype, ventral aspect. 38, ninth abdominal tergum, male, dorsal aspect. 39, subgenital plate, female paratype, ventral aspect. **Figs. 40-43.** *Panorpa reclusa* n. sp. 40, genital bulb of male holotype, right lateral aspect. 41, segments 9-11, male, ventral aspect, to show apparent fusion of basal segments of cerci to small tenth segment. 42, right dististyle, male holotype, posteroventral aspect. 43, ninth abdominal sternum and hypovalves, male, ventral aspect. **Figs. 44-49.** *Panorpa mucronata* n. sp. 44, genital bulb, male holotype, ventral aspect. 45, ninth abdominal tergum, male paratype, dorsal aspect. 46, subgenital plate, female, dorsal aspect. 47, terminal abdominal segments, female, right lateral aspect. 48, genital plates, female paratype, ventral aspect. 49, same, right lateral aspect. Scale a, figs. 37-47; scale b, figs. 48, 49.

eral lobes, in *contorta,* while it narrows noticeably past its mid-length, in *attenuata,* and has more narrowly rounded lateral lobes. While no distinctly green coloration can be seen in any of the available specimens of *attenuata* (only a trace in the tarsi of two individuals), Dr. Hanson recalls the specimens as "pale green" when alive.

Panorpa reclusa new species

Description based on one male, pinned.

Head: Dorsum yellowish brown except small ocellar triangle black; rostrum light yellowish brown, slightly darker at sides, labrum and lower clypeus retaining greenish pigment; maxillary palps yellowish brown; antennal scape yellowish brown, pedicel brown, flagellum brown, with 37 flagellomeres.

Thorax: Pronotum pale yellowish brown medially, darker at sides, with 5-6 conspicuous black setae at each side on anterior margin, 1-2 on posterior margin at each side of pale median band; mesonotum and metanotum uneven light brown with numerous short, black setae directed backward; pleura, coxae and mera yellowish brown, with scattered pale setae longest and most dense on anterior surfaces of coxae. Femora, tibiae and basitarsi yellowish brown, tarsomeres 2-5 slightly darker, major setae dark brown.

Wings tinged with gray-brown, with light brown markings; stigma brown; outer radial cells faintly darkened along wing margin, with diffuse brown spot from R_3 to R_5, more basal diffuse spot from R_5 to outer cell M_2; pterostigmal band represented by transverse spot from base of stigma to M_1, including outer nygma, and faint spot at end of M_4; spot extending from end of Cu_1 into proximal cell M_3; small darkening around proximal nygma, and faint spot between R_1 and R_2, both slightly beyond fork of Rs.

Abdomen of male: Terga 2-5 yellowish brown with short yellow hairs, corresponding sterna paler; segment 6 yellowish brown, posterior half of dorsum conspicuously concave, without hairs (area contacted by genital bulb when brought fully forward); segments 7-9 paler than 6, segments 8 and 9 (genital bulb) showing traces of green pigment. Notal organ weakly developed: low, rounded median prolongation of tergum 3 with downcurved, yellow hairs, and broad peg on anterior tergum 4 with forwardly curved, sclerotized apex. Hypovalves (Fig. 43) slender, of nearly uniform width throughout, extending slightly beyond ventral connection of basistyles, borne on short prolongation of ninth sternum. Tergum 9 abruptly narrowed at level of cerci (Fig. 41), with broadly U-shaped apical emargination; tergum thickened and strongly arched dorsad near mid-length (Fig. 40). Cerci apparently fused basally to sternum 10. Basistyles separated ventrally by only about 0.4 their length, with cluster of black setae on postero-ventral edge directed mesad. Outer margin of dististyles slightly concave before mid-length; basal cup prolonged ventromesally; sharp, strongly sclerotized point on mesal margin above cup, concealed by basal cup in ventral aspect; row of setae from base of cup toward apex (Fig. 42). Aedeagus complex (Fig. 36), ventral parameres dark yellowish brown, two-branched; ventral branch with brown tip; dorsal branch acutely tipped, with pale membranous appendage prolonged conspicuously in both directions from attachment. Dorsal parameres yellowish brown with sharp apex, sharp "tooth" near apex, and numerous small teeth near base opposite rounded, dorsal prominence. Ventral valves yellowish brown, long and slender; dorsal valves darker, rounded apically.

Measurements: Body length, male holotype, about 10.8 mm. Fore wing length 11.9 mm. Antenna about 9.1 mm.

Type: Holotype, male, collected 22 miles (35.2 km) northeast of Jacala, Hidalgo, Mexico, elevation 5300 feet (1615 m), 27 August 1972, by G. W. Byers and R. Thornhill; in the SEM. The genital bulb has been dissected and is in a microvial of glycerin on the pin with the rest of the specimen.

Panorpa reclusa was collected together with *P. mucronata* but is strikingly different in length of hypovalves, shape of basal cup of dististyles and overall length of genital bulb; it also differs in wing maculation. In general aspect of the genital bulb, *P. reclusa* more nearly resembles *P. contorta* of San Luis Potosí, but in details of the aedeagus it is altogether different (compare Figs. 25 and 36). No females could be associated with the male of *reclusa,* although I have six unidentified females with much more darkly marked wings, taken at the same locality in Hidalgo, in a much earlier season (mid-July). The male holotype differs in one way or another from all other species of the *involuta* group known, hence the name (Latin *reclusa* = alone, separated, removed).

Panorpa mucronata new species

Description based on 15 males, 7 females, pinned, and 5 males, 7 females in alcohol.

Head: Dorsum sordid yellowish brown except dark brown around ocelli; rostrum and frons below antennal bases light yellowish brown; mouthparts including maxillary palps yellowish brown. Scape pale yellowish brown, pedicel brown, flagellum dark brown with 35-36 flagellomeres (holotype 35).

Thorax: Pronotum light yellowish brown medially and at sides, brown dorsolaterally, especially on transverse ridges; 5-7 black setae at each side on anterior margin. Mesonotum and metanotum mainly light grayish brown, darker brown at sides before wing bases, covered with numerous short, black setae directed backward, but no large setae. Pleural surfaces, coxae and mera unevenly yellowish brown (variation due to post-mortem changes in drying), with scattered pale setae longest and most numerous on anterior surfaces of coxae. Femora pale yellowish brown (with faint greenish tinge in some specimens); tibiae and tarsi darker yellowish brown; basitarsus as long as tarsomeres 2-5 together in fore and middle legs, longer than 2-5 in hind legs.

Wings faintly tinged with grayish brown, markings light brown to brown. No complete bands and few spots; fore wings of males either with no distinct markings (e.g., holotype) or: diffuse clouding across outer cells R_3 to M_1, Ptb represented by spot at distal end of stigma and irregular spot from proximal end of stigma to M_{1+2} including outermost nygma, small spot from R_1 to R_{2+3} near level of FM, small spot at ORs and spot between Cu_1 and Cu_2 midway between cubital cross-veins. No dark borders along radial or medial cross-veins. Fore wing of female similar to that of more darkly marked males but often with spot at end of Cu_1 and faint spot at end of M_4.

Abdomen of male: Terga 2-5 unevenly yellowish brown with short, pale setae; corresponding sterna only slightly paler; segment 6 yellowish brown, its posterodorsal one-third somewhat concave, without setae (genital bulb contacts this surface when brought fully forward); segemnts 7-8 short; genital bulb (Fig. 44) elongate, pale grayish brown to tan, with greenish tinge in some males. Notal organ weakly developed: low, broadly rounded projection with downcurved, yellowish hairs, on tergum 3, and small peg with sclerotized, sharp tip curved cephalad, on tergum 4. Hypovalves (Fig. 44) unusually elongate, slender, extending nearly to ends of basistyles, separated basally by twice width of a hypovalve, or more, with yellowish hairs generally sparse but longer and much more dense near mid-length on mesal surface. Tergum 9 (Fig. 45) gradually narrowing toward apex, arched away from basistyles near its mid-length so much of dorsal parameres can be seen in side view; apex of tergum very slightly emarginate to truncate. Basistyles separated only about 40 per cent of their length in ventral aspect. Inner, posteroventral margin of each basistyle bearing 8-10 black setae directed mesally; similar setae on inner surface of basistyle in irregular diagonal row more dorsal at basal end. Outer margins of dististyles slightly concave near mid-length, evenly curved to strongly sclerotized tip; basal cup of dististyle shallowly concave on lower (anterior) surface, longer than wide, with strongly sclerotized apical margin slightly upturned to small mucronate point in most males (11 of 15; Fig. 44): (margin slightly upturned in males

lacking apical point). Inner margin of dististyle bearing sharp point concealed by basal cup in ventral aspect (cf. Fig. 42); uneven, short row of setae extending up ventral surface of dististyle from basal cup. Ventral parameres (Figs. 50, 51) two-branched, ventral branch pale yellowish but moderately sclerotized, flattened, obliquely truncate; dorsal branch yellowish, with thin, membranous dorsa margin (presumed equivalent to membranous appendage in related species). Dorsal parameres thickest at nearly 90-degree bend slightly before mid-length, well sclerotized but straw-yellow, with large, triangular, subapical "tooth" and smaller point at apex. Ventral valves short, moderately sclerotized, totally concealed in ventral aspect; dorsal valves short, bluntly rounded, well sclerotized.

Abdomen of female: Terga unevenly light brown to brown; corresponding sterna, particularly 2-5, somewhat paler. Subgenital plate (Figs. 46, 47) unusually elongate, prolonged posteriorly to narrowly rounded apex with dorsal surface of apical one-third well sclerotized and bearing scattered, minute setae; longer setae around margin. Genital plates small, with axial portion compressed, straight and slender in ventral aspect, thick in lateral aspect (Figs. 48, 49), with anterior apodemes turned slightly dorsad, not darkly sclerotized; length of apodemes variable; apical plate curved ventrad at sides, pale yellowish brown; basal plate only weakly developed, curved closely around axial portion, its anterior margin indistinct.

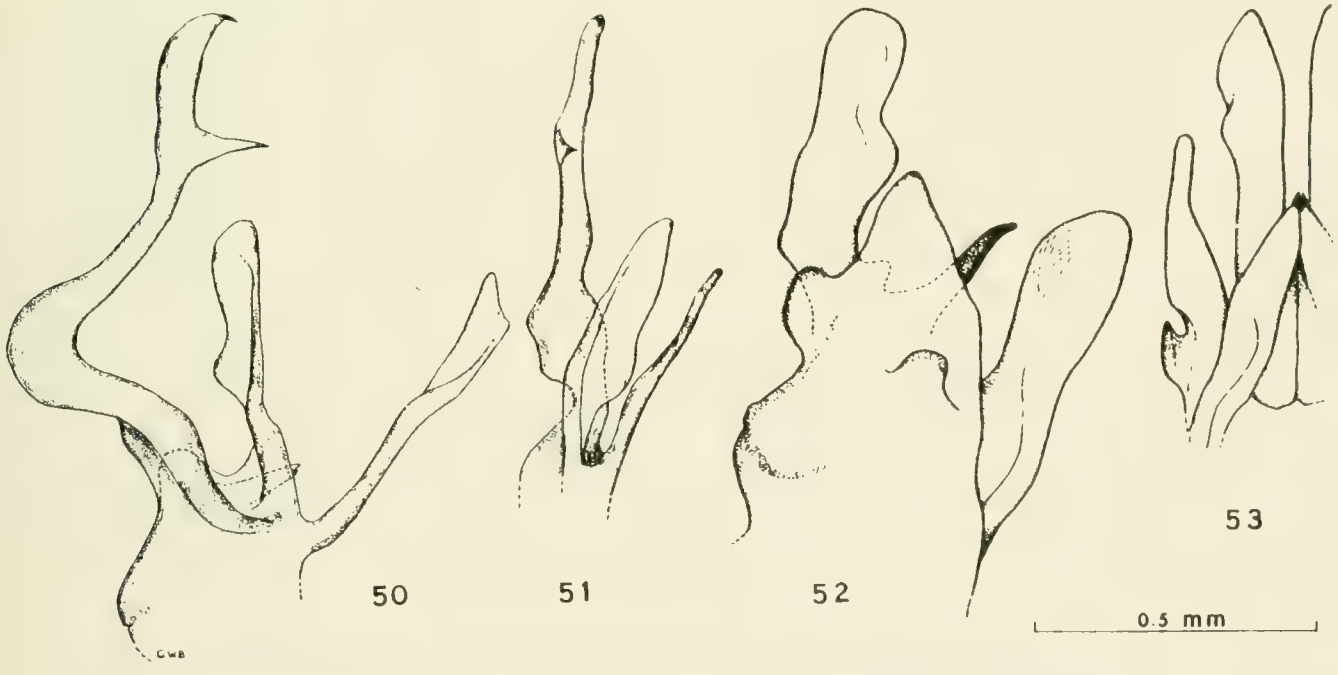
Measurements: Body length (based on pinned specimens), male, about 8.8-12.5 mm (holotype 9.9 mm); female, 9.2-10.3 mm (allotype 9.0 mm). Length of fore wing, male, 11.0-11.9 mm (holotype 11.4 mm); female, 10.6-11.9 mm (allotype 11.9 mm). Antennal length, male, about 8.5 mm, female about 8.4 mm.

Types: Holotype, male, collected beside Highway 85 (Interamerican Highway) at El Ocote vicinity, 22 miles (35 km) by road northeast of Jacala, Hidalgo, Mexico, elev. 5300 ft. (1618 m), 27 August 1972, by G. W. Byers and R. Thornhill (GWB field cat. Hidalgo no. 16). Allotype, female, and 3 male, 1 female paratypes same data as holotype. Additional paratypes: 10 males, 10 females, same locality as holotype, 18 July 1963, G. W. Byers (cat. no. 11); 2 males collected at Minas Viejas, Hidalgo, 4 August 1966, by) O. S. Flint, Jr., and M. Ortiz. Holotype, allotype and most paratypes are in the SEM; 2 paratypes in the USNM.

The habitat at the type locality was the edge of a forest of various broad-leaved trees (mainly oaks, beech, alder), at the foot of a north-facing slope, with underbrush of brambles, thorny vines, bracken-like ferns and scattered patches of herbaceous plants. The Panorpas were found on the broad-leaved herbaceous plants or less often on brambles, 2-3 feet above the ground, at edges of open areas but in places that would have been shaded on a sunny day. (It was 100% overcast, foggy and a cool 70°F when the first collection was made, 67° the next.) *P. mucronata* appeared to be early in its season of emergence on 18 July, as some individuals were callow on that date (therefore preserved in alcohol). When at rest, *P. mucronata* holds its wings roof-like above the body, that is, not flat and overlapped.

When alive, this species has a bright green color, particularly evident on the thoracic and abdominal pleura (see comments under *Panorpa involuta*), which fades rapidly in alcohol-preserved specimens and in a few hours or days in dried specimens.

Males of *Panorpa mucronata* can be recognized readily by the long, slender, deeply divided hypovalves and, usually, by the mucronate tips on the basal cups of the dististyles, for which the species is named. A male lacking the sharp tips on the basal cups of the dististyles was dissected, and the aedeagus characteristic of the species was also found in this male. The obliquely truncate ventral branches of the ventral parameres can usually be seen in an intact, dried in-



Figs. 50-51. *Panorpa mucronata* n. sp. 50, aedeagus, male paratype, left lateral aspect. 51, left half of male aedeagus, ventral aspect. **Figs. 52-53.** *Panorpa bimacula* n. sp. 52, aedeagus, male paratype, left lateral aspect. 53, left half of aedeagus, ventral aspect. Scale, all figures.

dividual. Females are also easily recognized by the unique elongate and narrow-tipped subgenital plate.

Key to Species in the *Panorpa involuta* group

1. Wing pattern of two spots: a triangular, dark brown pterostigmal spot from C to near M_1 and an uninterrupted, dark brown apical spot or band from R_2 to M_1; wing otherwise clear ..... *ramosa*
—. Wing pattern with more than two spots or bands or without distinct markings 2
2. Pterostigmal band (ptb) complete from C to hind margin; apical band divided by clear area into two transverse, curved bands, one along apical margin, one more proximal; two additional large spots between ptb and wing base, one at posterior margin, one near costal margin; hypovalves of male slender, about 8 times as long as basal width, borne on subtriangular extension of ninth sternum ..... *mexicana* Banks
—. Pterostigmal and apical bands fragmented (or ptb complete in some females of *P. involuta*, with more than two spots between ptb and wing base) 3
3. Male hypovalves (hv) deeply separated, long (about 12-13 times as long as basal width), extending far beyond connection between basistyles; basal cup of dististyle with strongly sclerotized mesal margin, usually with upturned point; subgenital plate of female narrowed and prolonged backward, with narrowly rounded apex ..... *mucronata*
—. Male hv short, not reaching edge of connection between basistyles or only slightly beyond edge; subgenital plate of female not narrowly rounded at apex 4
4. Male hv short, slender, curving apart and each tapering to narrow apex; inner margin of basistyle conspicuously indented; subgenital plate of female oval in outline, shallowly notched apically ..... *attenuata*
—. Male hv extending to or slightly beyond connection between basistyles, if slender not attenuate toward apex; subgenital plate of female widened posteriorly (female of *P. reclusa* unknown) 5
5. Male hv deeply separated; ninth sternum bearing hypovalves not conspicuously prolonged beneath genital bulb; subgenital plate of female with small median projection in emargination between broadly rounded apical lobes ..... *contorta*
—. Male hv borne on narrow prolongation of ninth sternum; subgenital plate of female broadly rounded apically *(involuta)* 6
6. Male hv shorter than prolongation of ninth sternum (ventral aspect); aedeagus as Figs. 22, 23; subgenital plate of female broadly rounded apically ..... *involuta*
—. Male hv longer than prolongation of ninth sternum (ventral aspect); aedeagus as Fig. 36; female unknown ..... *reclusa*

Panorpa bimacula new species

Description based on 65 males, 44 females, pinned, and 14 males, 46 females preserved in alcohol.

Head: Dorsum dark yellowish brown except brownish black around ocelli; rostrum yellowish brown at sides and medially, with two amber brown vertical (longitudinal) stripes. Mouthparts amber brown; terminal segment of maxillary palps dark brown. Antennal scape light yellowish brown, pedicel brown; flagellum black, with 42 to 47 flagellomeres (42 on left side, 43 on right side in holotype).

Thorax: Pronotum yellowish brown medially and at sides, with two irregular, broad black spots or longitudinal bands intervening; anterior margin strongly upturned, with 9-12 conspicuous marginal black setae and numerous shorter black setae at each side. Mesonotum black at each side, with broad yellowish brown to light brown median band continuous with pale medial portion of pronotum and gradually widening posteriorly to include entire scutellum. Numerous short, recumbent black setae on most of mesonotal surface. Metanotum sordid yellowish brown medially, with large, diffuse black spot at base of each hind wing; setae paler and more sparse than those of mesonotum. Pleural surfaces, coxae and mera unevenly yellowish brown, with setae darkest and most dense on anterior surfaces of coxae. Ventral tips of mesothoracic and metathoracic mera diverging slightly from respective coxae. Femora and tibiae yellowish brown with encircling rows of dark, appressed setae; tarsi slightly darker than tibiae; larger setae of tibiae and tarsi black.

Wings (Fig. 99b) mostly hyaline, with two conspicuous dark brown or grayish brown spots on each, one terminal, one pterostigmal. Extent of spots variable even among wings of one individual; pterostigmal spot often extending back to nygma between veins R_5 and M_1. Small, weak spot on vein M_4 in fore wings of some individuals (e.g., holotype); less often a small spot in second cell Cu_1 of fore wing. Numerous dark microsetae in nearly all cells of fore wing, on upper surface.

Abdomen of male: Segments 2-5 unevenly yellowish brown, segments 6-9 darker yellowish brown. Segments 7 and 8 short, thick. Notal organ a slightly elevated and extended, broadly rounded caudal margin on tergum 3, with downcurved, yellow setae, and a small, median peg (normally concealed) on tergum 4. Hypovalves of ninth sternum (Fig. 54) short, slender, divergent from common stem, with conspicuous yellow hairs along mesal margin of distal two-thirds of each. Tergum 9 narrowed beyond level of projecting cerci, weakly bilobed apically (Fig. 55). Outer margins of dististyles, in ventral aspect, slightly concave in basal half, slightly convex in apical half except more strongly curved close to darkly sclerotized apex. Basal cup of dististyle shallowly concave on anterodorsal surface; ventral margin with long, yellow hairs. Ventral parameres (Figs. 52, 53) pale, compressed, rounded apically, inclined together with apices in contact. Dorsal parameres similarly pale, enlarged, rounded apically. Ventral valves of aedeagus dark, slender, with acute tips. Lateral processes large, conspicuous in ventral aspect.

Abdomen of female: Terga 2-6 dark yellowish brown (often with uneven post-mortem darkening), corresponding sterna paler yellowish brown. Segments 7-10 evenly dark yellowish brown. Subgenital plate of sternum 8 (Fig. 56) broadly rounded apically, with shallow median notch and about ten large, dark setae on or near margin at each side of notch (9 and 10 in allotype), lateral setae shorter, paler. Genital plates (Fig. 68) reduced to thick, nearly straight axial portion with hyaline apex, anterior apodemes moderately divergent; apical plate rounded posteriorly at each side, only weakly developed anteriorly; basal plate not evident.

Measurements: Body length (based on pinned specimens), male, 9.3-11.8 mm (holotype 11.2 mm); female, 10.1-13.8 mm (allotype 11.0 mm). Length of fore wing, male, 12.6-14.1 mm (holotype 13.9 mm); female, 13.0-15.2 mm (allotype 13.2 mm). Antennal length, holotype, about 11.8 mm; allotype about 11.0 mm.

Types: Holotype, male, allotype and 22 male, 12 female paratypes, pinned, and 4 male, 32 female paratypes in alcohol, collected at El Tejocote, highway 190, at km 141 (about 50 km northwest of city of Oaxaca), elevation 2320 m, state of Oaxaca, Mexico, 4 August 1969, by G. W. Byers (field catalogue Oaxaca no. 10); in the SEM. Additional paratypes: same locality but 5 August 1969 (field cat. no. 12), 13 males, 8 females pinned, 6 males, 10 females in al-

cohol (SEM, USNM, MCZ and UMMZ); essentially same locality (labels read "Tejocates"), 4 August 1965, O. S. Flint and M. Ortiz (7 males, 5 females; USNM); same locality (labels read "Tejocotes"), 8 June 1967, O. S. Flint, Jr. (5 males, 7 females; USNM, SEM); Oaxaca, 3 km south of El Marques, 1 July 1990, Wes and Fred Bicha (12 males, 7 females; SEM and WB); same locality, 3 July 1990, Wes Bicha (8 males, 4 females; WB); same locality, 18 August 1993, Wes Bicha (1 male; WB); Oaxaca, 15.1 mi. N of San Gabriel Mixtepec, Hwy. 131, 3850 ft., 11 July 1987, R. Wharton (1 female; TAM); Oaxaca, Las Animas, 1 mi. N of El Punto, 7400 ft., 17 July 1987, R. Wharton (2 females; TAM); Puebla, 4.7 mi. SW of La Cumbre, 5100 ft., R. Wharton (1 female; TAM).

Panorpa bimacula was found together with *P. immaculata* Esben Petersen in shaded, low, broad-leaved herbaceous plants growing on fairly level ground near the highway (at El Tejocote) or low on nearby slopes, which were steep and wooded with oaks and some pines. Both species of *Panorpa,* I noted, remained near the ground, usually below 30 cm, uncommonly up to 45 cm, rarely to 60 cm. Several individuals were captured by hand in vegetation only 5-6 cm high. There was occasional light rain during the first collecting period, which may have influenced this behavior. The next day, the rain having ended, some of the Panorpas were higher in the vegetation (up to about 90 cm), although most were still found relatively near the ground. Again, a preference for broad-leaved plants was noted, the scorpionflies were never on nearby ferns or grasses.

The species takes its name (Latin *bi* = two, *macula* = spot) from its easy recognition characteristic, two conspicuous spots on each wing, but also from the two dark spots on the pronotum, two each on the mesonotum and metanotum and the two elongate spots on the front of the rostrum. At least four other Mexican species of *Panorpa* have some degree of gray coloration at the wing tips; these are *P. terminata* Klug, *P. penicillata* Byers, *P. ramosa* and *P. serta,* new species described herein. (There may be others, as yet undiscovered.) *Panorpa terminata,* however, rarely has any gray pigmentation near the pterostigma (a thin, weak, transverse subcrescentic spot near base of stigma seen in two females). Males of *P. serta* can easily be differentiated from those of *bimacula* by the elongate genital bulb with long, slender prolongation of the ninth sternum reaching the ends of the basistyles and only slightly divided near its apex (Fig. 57). *Panorpa penicillata* has no pattern of pigmentation on the thoracic dorsum, and males of this species have a small, setiferous branch on the ventral surface of each hypovalve and have the ninth abdominal tergum deeply bilobed. While *P. bimacula* is so far known only from Oaxaca, *terminata* occurs farther north (Morelos), and *penicillata* in the western mountains of Durango. *P. ramosa,* known only from Hidalgo and *P. serta* from Michoacan, differ from *bimacula* in several characteristics as discussed in the sections on these species.

Panorpa serta new species

Description based on 16 males, 11 females, pinned.

Head: Dorsum yellowish brown; diffuse brown spot on vertex at edge of each eye, usually a light brown spot between this and piceous ocellar triangle; lateral ocelli 1.3 times as wide as median ocellus. Rostrum yellowish brown medially, darker at sides; mouthparts amber-brown except maxillary palps unevenly yellowish brown. Antennal scape pale yellowish brown, pedicel wholly or partly brown, flagellum brown to almost black, with 38-44 flagellomeres.

Thorax: Pronotum mostly black, pale yellowish along posterior margin and small median spot on anterior margin; 9-10 black setae at each side on anterior margin. Mesonotum and metanotum with broad, pale yellowish brown band medially, with numerous short, black hairs directed caudad; dark brown to nearly black at sides except small pale spot near wing base in most individuals. Pleural surfaces, coxae and mera unevenly pale yellowish brown with numerous short, dark setae on anterior coxa and on mesothoracic coxa and episternum; sparse, pale setae on metathorax, most numerous on coxa; small, intensely black spot at each end of mesepimeron and lower end of metepimeron. Femora and tarsi yellowish brown, tibiae slightly paler, all with yellowish hairs but major setae black.

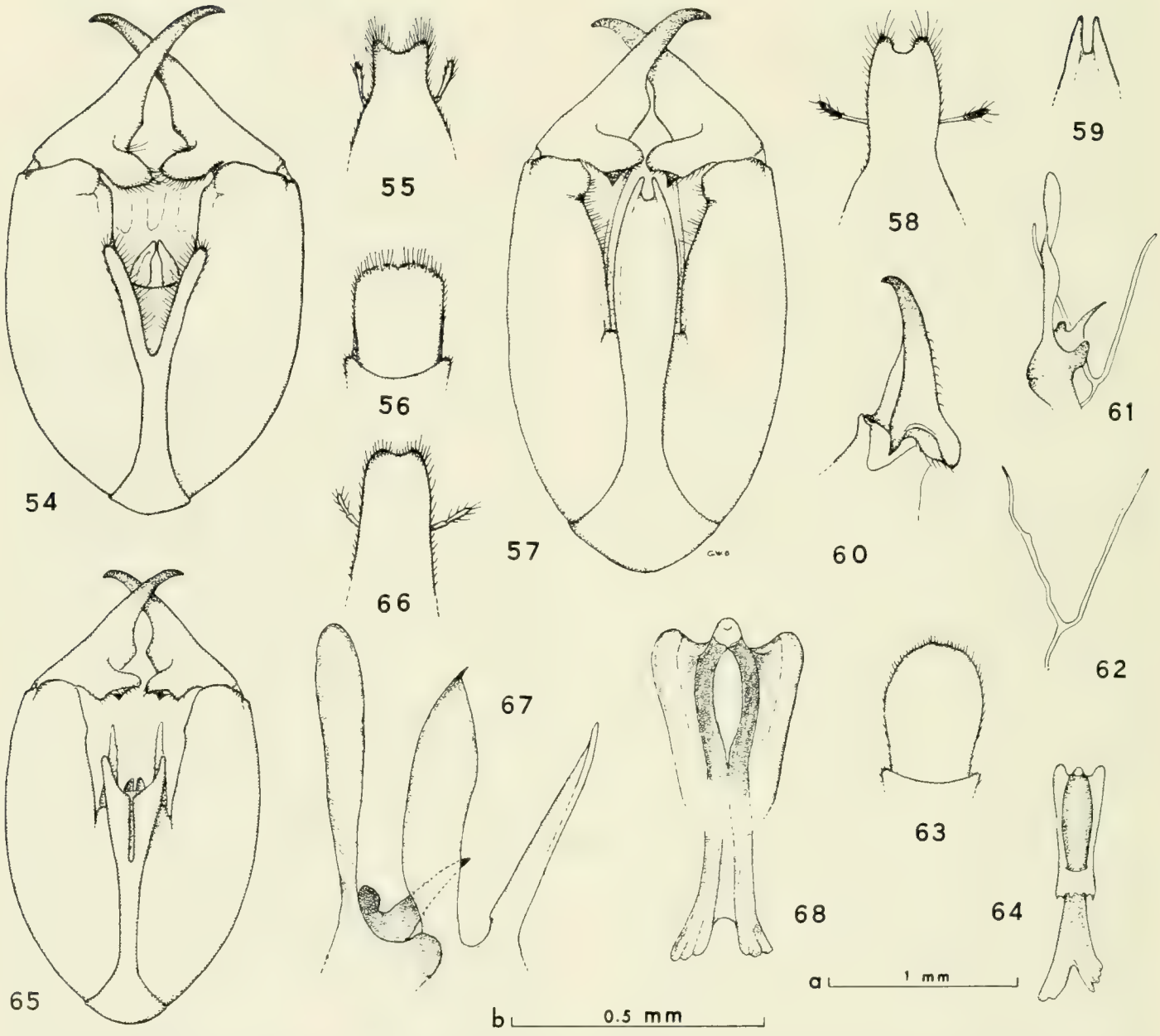
Wings faintly tinged with gray-brown, slightly iridescent, stigma dark yellowish, apical spot brown, most veins brown, some outer cross-veins, humeral cross-vein, basal stem of Cu and thyridium at first fork of M white; abundant microsetae in all cells of fore wing; apical spot variable in extent, usually from R_2 to M_1.

Abdomen of male: Terga 2-5 unevenly yellowish brown, corresponding sterna slightly paler; segment 6 yellowish brown with abundant short, pale setae. Notal organ a broadly rounded, slight median prolongation of tergum 3 with downcurved, yellowish hairs, and roughly triangular prominence on tergum 4 with strongly sclerotized apex curved cephalad. Segments 7-8 short, together about as long as 6, yellowish brown. Genital bulb elongate, including dististyles nearly as long as head, dark yellowish brown. Hypovalves (Fig. 57) extending to ends of basistyles, fused nearly their complete length, producing structure somewhat thickened along outwardly curved sides, thin and translucent between; depth of apical notch and width of combined hypovalves variable. Ninth tergum (Fig. 58) with rounded apical lobes separated by shallow emargination; cerci with only one exposed segment, slender basally, expanded and darkened apically. Basistyles separated ventrally less than half their length. Outer margins of dististyles straight until subapical curvature to strongly sclerotized tip. Basal cup of dististyle (Fig. 60) projecting ventro-mesally, underside shallowly concave, densely sclerotized at apical margin, along dorsal margin and onto acutely pointed projection on dorsal edge of cup (apparently homologous with sclerotized point more removed from basal cup in some other Mexican species). Ventral parameres (Figs. 61, 62), yellow, two-branched, both branches long, slender except for slight widening near mid-length of dorsal branch; ventral branches approximately parallel to edges of fused hypovalves. Dorsal parameres elongate, flattened, rounded at apex, twisted near mid-length, yellowish but moderately sclerotized. Ventral valves slender, acutely tipped, moderately sclerotized; dorsal valves short, bluntly rounded at apex.

Abdomen of female: Terga 2-9 mostly unevenly brown with diffuse, narrow, paler median stripe; sterna much paler than corresponding terga; segment 10 light brown, cerci black. Subgenital plate (Fig. 63) broadly rounded at apex, with only pale hairs. Genital plates (Fig. 64) only slightly expanded from axial portion; apical plate with narrowly rounded posterior lobes; basal plate indistinct, mostly membranous; anterior apodemes moderately divergent, much paler than posterior part of axial structure.

Measurements: Body length, male, about 10.2-13.2 mm (holotype 11.0 mm); female, about 11.9-13.5 mm (allotype 13.1 mm). Length of fore wing, male, 13.3-14.4 mm (holotype 14.1 mm); female, 13.0-14.2 mm (allotype 13.9 mm). Antennal length, male, about 10.8 mm, female, 10.5 mm.

Types: Holotype, male, allotype female and 12 male, 10 female paratypes collected 16.4 miles (26.2 km) east of Morelia, Michoacán, Mexico, elevation 7000 ft. (2134 m), 9 August 1963, by George W. Byers (GWB field catalogue Michoacán no. 1); 3 male paratypes, Michoacán, jct. Hwy. 4 and Huetano Road, 5 miles (8 km) east of Morelia, 2100 m, 8 July 1947, T. H. Hubbell no. 83 (earlier misidentified by me [Byers, 1958] as *P. terminata*). Holo-



Figs. 54-56, 68. *Panorpa bimacula* n. sp. 54, genital bulb, male paratype, ventral aspect. 55, ninth abdominal tergum, male, dorsal aspect. 56, subgenital plate, female, ventral aspect. **Figs. 57-64.** *Panorpa serta* n. sp. 57, genital bulb, male holotype, ventral aspect. 58, ninth abdominal tergum, male, dorsal aspect. 59, apex of fused hypovalves, showing variation from Fig. 57. 60, right dististyle and apex of basistyle, mesal aspect. 61, aedeagus of male, left or near ventral paramere removed, left lateral aspect. 62, ventral paramere, left lateral aspect. 63, subgenital plate, female, ventral aspect. 64, genital plates, female, ventral aspect. **Figs. 65-67.** *Panorpa terminata*, male from Morelos, Mexico. 65, genital bulb, ventral aspect. 66, ninth abdominal tergum, dorsal aspect. 67, aedeagus, left lateral aspect. Scale a, figs. 54-66; scale b, figs. 67, 68.

type, allotype and most paratypes are in the SEM. Paratypes also in USNM, UMMZ and collection of WB.

The type locality is a mountain pass, the Puerto Presidente Ortiz Rubio, on Highway 15. The general habitat was pine forest with occasional oaks, underbrush of *Baccharis*, small oaks, thorny leguminous shrubs, some patches of *Rubus*, wide patches of flowering *Lythrum*, etc. The Panorpas were on broad-leaved herbaceous plants growing on relatively flat "terraces" on the slope. Three species of *Panorpa* were present and in such numbers that 32 were collected in half an hour before a downpour of rain ended collecting; sky overcast, temperature 67°F.

Superficially, *P. serta* closely resembles *P. terminata* but is slightly larger and darker; the similarity is particularly in the wing markings and pale median stripe on the thorax. The slight separation of the hypovalves occurs also in *P. immaculata* Esben Petersen, but in that species the prolongation of sternum 9 is extremely slender and does not give the impression of fused hypovalves, rather only short ones on a long pedicel; and its wings are unmarked. While males of *P. serta* can readily be distinguished from those of any other species by the long, fused hypovalves (Latin *serta* = joined, connected), females are not as easy to differentiate from *terminata, ramosa* or *bimacula,* species with similar wing markings. Identification may require dissection.

Panorpa terminata Klug

This is a common species in Morelos, Mexico, but I have not collected it in other parts of the country. Many years ago (Byers, 1958) I identified three specimens collected in Michoacán by T. H. Hubbell as *terminata,* but I have recently re-examined them and they belong to the species *P. serta* described above. When I compared a female of *serta* with the female types of *terminata,* I noted that my specimen was somewhat larger and had more darkly marked wings than typical *terminata.*

The male of *P. terminata* has never been described. In addition to the characteristic wing markings, it has hypovalves that set it apart from other species (Fig. 65); borne on a slender pedicel, they widen to slightly beyond mid-length, then narrow toward the tips. Tergum 9 (Fig. 66) has two rounded and somewhat darkened apical lobes separated by a shallow emargination. The aedeagus (Fig. 67) is unlike that of any other species, particularly in the shapes of the dorsal parameres and the dorsal branch of the ventral parameres.

On 29 and 30 July 1963, I collected numerous individuals of *P. terminata* in early morning and late afternoon, at a site about 23 km by road north of Cuernavaca, elevation 2225 m. It seemed this species spent much of the day very low in the vegetation or on the ground. No Panorpas were observed at this site between 2 and 5 p.m., and only three were found in two hours of general collecting, 9-11 a.m. However, before 9 a.m. and after 5:15 p.m. they were commonly seen and netted about 45-60 cm above ground surface, on broad-leaved herbaceous plants and bunch-grasses shaded by oak and pine trees. On another occasion, I noted that when the sky was totally cloudy-overcast, the Panorpas were more active in the vegetation during the day, but when suddenly alarmed they flew to the ground, or near it, not to other leaves well above the surface.

This species' original description (Klug, 1836: 106, fig. 10) was based on three female specimens, all of which are still present in the collection of the Zoologisches Museum, Humboldt University, Berlin. All three have green labels reading "Mexico, Deppe." Two are also labelled "*Panorpa terminata* Kl." and, on a small red tag, "Type," and the third has the red type label and a small label with the printed number "237." The number 237 refers to an entry for *Panorpa terminata* Klug (3 Ex., Mexico, Deppe) in the "Catalogus Generalis Musei Zoologici Berolinensis, Band Neuroptera." I am indebted to Dr. K. K. Günther for this information. One of the syntypes has had the wings spread (photo in the monograph by Esben-Petersen, 1921: 71, fig. 75). This female is now designated lectotype of *P. terminata* and has been so labelled. It is intact except the flagellum of its right antenna is missing, and the right hind leg and adjacent portion of the thorax have been destroyed (by dermestid?). The description accompanying Esben-Petersen's photograph is based on a specimen from Tepic, Nayarit, and probably pertains to *Panorpa penicillata,* as it mentions a "dark smoky, brown, subtriangular" pterostigmal spot extending halfway across the wing.

In the Museum of Comparative Zoology, Harvard University, there is a female specimen labelled "Hagen" and "Type, 11116" (on a red label), also "*terminata* Kl., Mexico." This is apparently not part of Klug's original type series and therefore is not a type.

There is a species in Michoacán, *P. serta,* that in many respects closely resembles *P. terminata* in coloration of body and wings. Its dorsal thoracic pattern in particular resembles that of *terminata.* Its females are slightly larger and darker than those of the type series of *terminata.* The genital bulbs of the males, however, are quite different (compare Figs. 65 and 57). The recorded travels of the collector of *terminata,* Ferdinand Deppe, add some support to my identification of the species from Michoacán. There is no indication that Deppe travelled to the west of Mexico City beyond Toluca (see Papavero, 1971: 103), while he crossed the modern state of Morelos on various trips, 1824-1827. And in Morelos, a species that agrees with the lectotype of *terminata* in characteristics of both size and coloration is quite common, and I have so identified it.

Bittacus disternum new species

Description based on 4 males, 7 females, pinned, one male in alcohol.

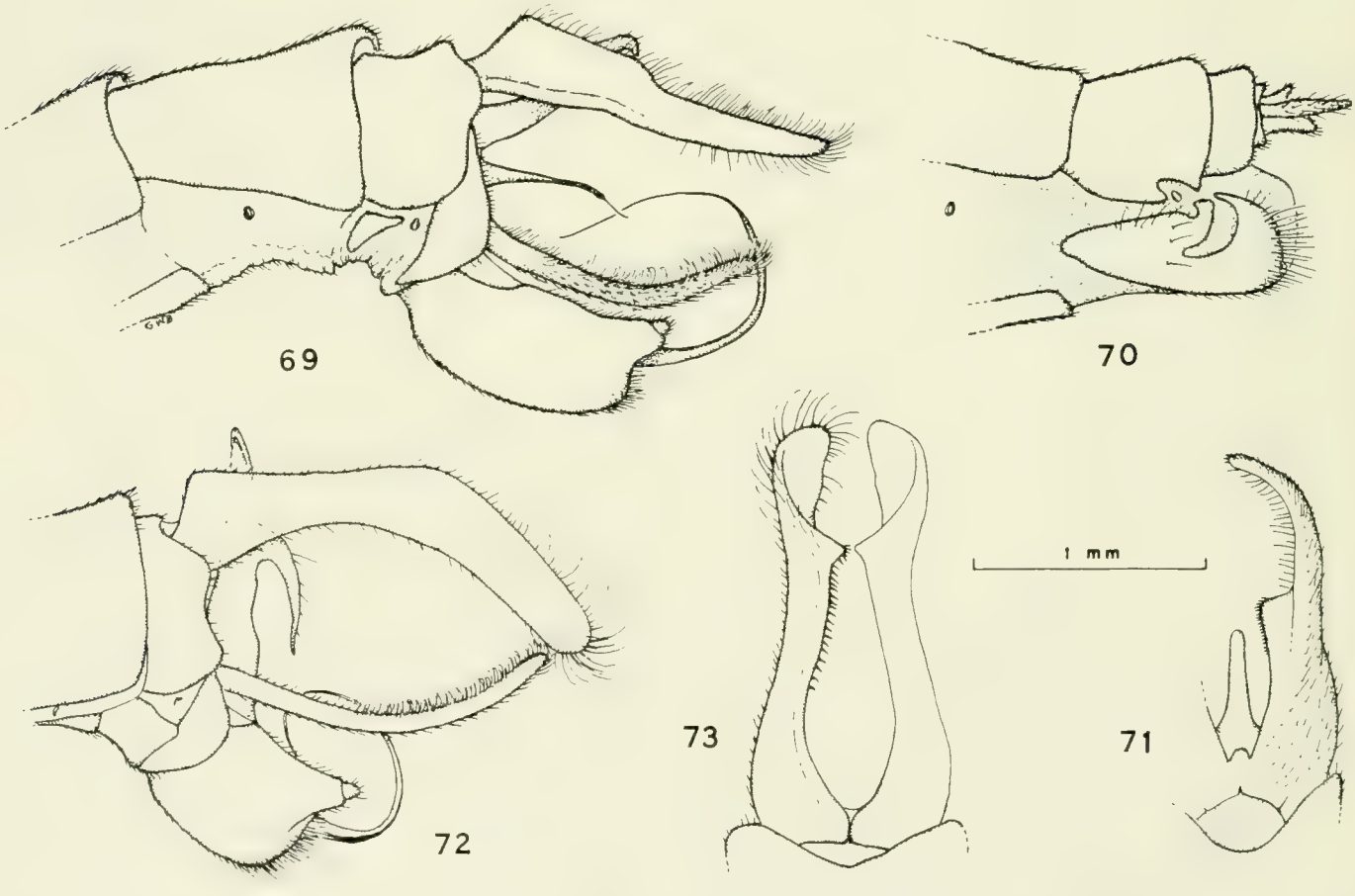
Head: Dorsum and frons unevenly brown, black around strongly protruding ocelli; diameter of lateral ocelli about 1.7 that of median ocellus. Rostrum and mouthparts dark brown; maxillary palps brownish black. Antennal scape and pedicel brown, less often yellowish brown; flagellum light brown with 21-22 flagellomeres with hairs slightly longer than diameter of respective flagellomeres.

Thorax: Pronotum unevenly brown, lightest brown along posterior edge; four conspicuous black setae on anterior margin, one dorsolateral, one lateral, on each side (rarely double in either position), each on slight elevation; two setae on posterior margin. Anterior propleura large, discoidal, with short setae along anterior edge, extending backward beneath lateral edges of pronotum. Anterior spiracle in vertical alignment with posterior pronotal margin. Mesonotum and metanotum unevenly brown, darkest on elevated areas, with one large, black seta on mesoscutum near base of fore wing, another on uppermost pleuron just before wing base; two smaller setae on each scutellum. Pleural surfaces, coxae and mera light brown, darkest on anterior mesepisternum, with scattered pale hairs most numerous on anterior surfaces of fore and middle coxae; three large, dark setae vertically aligned on posterolateral surface of hind coxa. Femora and tibiae dark yellowish brown with narrowly blackened tips; tarsi brown; hind femora of male slightly thickened near mid-length.

Wings tinged with grayish brown, stigma only slightly darker than membrane generally; indistinct darker clouding along most cross-veins, at origin of radial sector (ORs), at nearly perpendicular origin of R_{2+3} from Rs, at origin of media (OM), along diagonal line of cross-veins from fork of R_{4+5} to end of Cu_2, and at end of R_5 at somewhat pointed apex of wing. Scv beyond ORs; two pterostigmal cross-veins; no apical cross-vein between Cu_2 and 1A. Six conspicuous black setae along posterior margin of fore wing between wing base and end of vein 2A; fewer (usually 4) along similar margin of hind wing. Outermost radial and medial cells narrowed near apex of wing. Pale thyridium at first fork of M.

Abdomen of male: Terga 2-7 unevenly light brown to brown with short, pale hairs; tergum 8 slightly darker brown than preceding terga or epiandrial appendages; sterna 2-6 narrow, slightly paler than corresponding terga. Sternum 7 only weakly sclerotized (Fig. 69); sternum 8 membranous ventrally, with small, subtriangular sclerite at each side; sternum 9 normally developed at sides but completely divided ventrally by membrane. Epiandrial appendages extending well beyond basistyles, in lateral aspect abruptly narrowed shortly before mid-length, then tapering toward apex, apical one-third curved mesad; long, slender dark brown to black setae along dorsal and ventral margins, ventral ones inclined mesad; 3-5 short, thick black setae at apex. Diagonal shelf or ridge on mesal surface of each epiandrial appendage, beginning near anterior dorsal margin and widening backward toward abruptly transverse posterior edge (Fig. 71); shelf smooth, without setae on dorsal surface, bare surface also extending along dorso-mesal part of appendage; about 15 short, recurved black spines (thick at base, with acuminate tip) on mesal edge of lower, posterior one-third of shelf; 3-4 similar spines on mesal surface of appendage below shelf. Basistyles dark brown, about twice as long as dorso-ventral width; long setae at posterior end, fewer along dorsal edge. Dististyles short, inwardly curved, bluntly rounded at tips. Cerci about as long as epiandrial appendages, with numerous recurved, blackish brown setae on dorsal and mesal surfaces from about mid-length to apex. Upper branch of proctiger arched at tip, with long, black apical setae directed ventrad; lower branch slender, filiform near tip. Aedeagus slender near base, not coiled, filiform in approximately apical half.

Abdomen of female: Terga 2-8 unevenly light brown to brown with short, pale hairs; sterna slightly wider than in male, paler than corresponding terga; pleura light grayish brown. (Two teneral females not used in color description.) Tergum 8 (Fig. 70) notched at each side; eighth abdominal spiracle in this notch. Sternum 8 completely divided ventrally, sides bluntly pointed anteriorly, widely separated by membrane, separation narrowing posteriorly; broad connection between sternal plate and respective half of subgenital plate, with subcrescentic, membranous dorsolateral separation. Halves of subgenital plate narrowly separated ventrally (with membrane extending beyond posterior margin in specimen softened in de-



Figs. 69-71. *Buttacus disternum* n. sp. 69, terminal abdominal segments, male paratype, left lateral aspect. 70, terminal abdominal segments, female paratype, left lateral aspect. 71, left epiandrial appendage and proctiger, dorsal aspect. **Figs. 72-73.** *Buttacus sylvaticus* n. sp., male holotype. 72, terminal abdominal segments, left lateral aspect. 73, epiandrial appendages, dorsal aspect (most hairs omitted). Scale, all figures.

tergent); numerous stiff, black setae on and near posterior margin. Eggs cuboidal, with surfaces circularly impressed.

Measurements: Body length, male, about 19-20.5 mm (holotype 19 mm); female, about 10-19 mm (allotype 17 mm). Length of fore wing, male, 21.1-22.0 mm (holotype 21.6 mm); female, 19.6-21.0 mm (allotype 21.0 mm). Antennal length about 8.2-8.5 mm.

Types: Holotype, male, collected at Monteverde, elev. 1280 m, Puntarenas Province, Costa Rica, 26 May 1989, by J. S. Ashe, R. W. Brooks and R. A. Leschen (Snow Entomological Museum Costa Rica Expedition, no. 488), in SEM. Allotype female, 2 male and 2 female paratypes same data as holotype; same, except one male in flight intercept trap, 24 May 1989 (SEM). Additional paratypes, all from Costa Rica: Monteverde vicinity, 1400-1700 m, Erwin and Hevel Central America Expedition, 6-14 June 1973 (1 male; USNM); Cartago Prov., Turrialba, Centro Agronómico Tropical de Investigación y Enseñaza, 26-29 June 1986, G. E. Bohart and W. J. Hanson (1 female; Utah State University); Turrialba, Instituto Interamericano de Ciencias Agricolas, at light, 9 p.m., 10 September 1964, R. B. Roberts (1 female, SEM); Turrialba, at light, 27 July and 8 August 1965, G. C. Eickwort (2 teneral females, SEM).

At the type locality, the bittacids were collected from herbaceous plants on a shaded, flat area near a small stream, and all (of collection no. 488) were found within a small area estimated to be 15 x 30 feet (4.5 x 6.1 m).

Bittacus disternum is the only known species in the genus that has the eighth and ninth sterna in the male completely divided by membrane; hence the name (Latin *di* = separate + sternum). Long cerci occur in males of some other Central American and Mexican species of *Bittacus*, but none of these has epiandrial appendages resembling those of *B. disternum*. The eighth tergum and sternum and the subgenital plates of the female of *B. disternum* are also of a shape not seen in any other species. The wings are unlike those of other bittacids in their peculiar pattern of clouding and the narrowing of radial and medial cells near the apex.

Bittacus sylvaticus new species

Description based on two males, pinned.

Head: Dorsum and frons sordid yellowish brown, ocellar prominence dark brown to black; diameter of lateral ocelli 1.8-2.0 times that of median ocellus. Rostrum yellowish brown basally, amber-brown apically, dark reddish brown between; mouthparts amber-brown except maxillary palps brown. Antennal scape, pedicel and flagellum light brown; 21-22 flagellomeres, indistinct beyond 16 or 17, with hairs about as long as diameter of more basal flagellomeres, 5 times diameter on outer ones.

Thorax: Anterior propleura dark brown, roughly semicircular, their posterior edges beneath pronotum. Pronotum dark yellowish brown medially, unevenly darker brown at sides; one conspicuous black seta at each side on anterior margin, one on each side near posterior margin, the two setae in longitudinal alignment. Mesonotum unevenly light brown in slightly depressed median areas and on scutellum, darker brown on sides and anteriorly, with few very short hairs; one long, black seta near wing base, two smaller setae on scutellum; metanotum paler than mesonotum and without setae near wing bases. Mesothoracic pleura, coxae and mera unevenly grayish brown, darkest on episternum, palest on epimeron; scattered pale hairs longest and most dense on anterior surface of coxae; anepisternum slightly raised, with two black setae; metathoracic pleura, coxae and mera light brown. Femora dark yellowish brown to grayish brown, dark brown at apex; hind femora not expanded; tibiae yellowish brown, brown at apex, with yellow hairs and sparse black setae; tarsi yellowish brown with dark reddish brown claws.

Wings tinged with smoky brown, stigma and markings brown; apex of wing forming approximately a right angle at end of vein R_5. Diffuse spots at ORs, FRs, OM, surrounding pale thyridium at FM, in medial cells and in outer radial cells, especially outer cell R_4 at wing tip; diagonal darkened band from first r cross-vein across r-m, first m, around small thyridium at origin of M_4 and across m-cu. Diffuse spots enclosing both pterostigmal cross-veins, along r_2-r_3 cross-veins, at end of Cu_2 and along posterior medial cross-veins.

Abdomen of male: Terga 2-5 unevenly dark yellowish brown to brown, with short yellowish setae; tergum 2 with 4-5 conspicuous black setae along each lateral margin and light brown spot narrowly bordered with dark brown on each side at anterior end; sterna 2-5 long and slender, drawn up beneath terga in dried specimens, 2-4 pale yellowish brown to tan, 5 somewhat darker. Tergum 6 only about 0.7 as long as 5, and 7 only 0.4 as long as 5; both darker than 2-5. Sterna 6-7 short, brown, with tan markings on 7; sterna 8-9 membranous medially, together shorter than sternum 7. Tergum 8 short, broadly emarginate dorsomedially. Epiandrial appendages (Figs. 72, 73) dark brown, about four times length of basistyles, apical half strongly downcurved with dorsal margins rotated laterad so mesal face becomes largely dorsal; hairs increasing in length toward apex; low, rounded, transverse ridge on mesal face of each appendage at level of rotation, with short, curved, black spines at highest point of ridge; about 15-20 longer black spines, curved cephalad, near dorsal margin (but at different levels so exact count difficult) between transverse ridge and widest separation of appendages. Basistyles short, their dorso-ventral width about equal to length; short brush of hairs on postero-ventral margin. Dististyles short, curved inward, flattened and slightly expanded at apex. Cerci nearly as long as epiandrial appendages, pale tan, with short hairs on ventral surface, abundant longer, recurved hairs on dorsal surface except near base. Upper branch of proctiger protruding between bases of epiandrial appendages, bifurcate at apex; lower branch slender, tapering. Aedeagus unmodified, not greatly expanded at base, filiform in approximately apical half, not coiled.

Measurements: Body length, male, about 20.0-21.0 mm (holotype 21 mm). Length of fore wing 21.9-23.0 mm (holotype 23.0 mm). Antennal length about 7.1 mm.

Types: Holotype, male, collected in cloud forest 4.8 miles (7.7 km) northeast of Coscomatepec, Veracruz, Mexico, elevation abut 1420 m, on 8 August 1969, by G. W. Byers (field cat. Veracruz no. 17). Paratype, one male, same locality, collected 22-23 July 1966, by O. S. Flint, Jr., and M. Ortiz. The holotype is in the SEM, the paratype in the USNM.

The habitat at the type locality is described and its subsequent alteration discussed under *Panorpa involuta*, above. This new *Bittacus*, the new *Panorpa* and a new species of *Kalobittacus* (Byers, 1994) were all found during the first half-hour of collecting in this remarkable habitat. The name of the new *Bittacus* (Latin *sylvaticus* = of the forest) refers to the deeply shaded, cool and moist habitat in which the species was found, most Mexican bittacids being found in much lower, drier and warmer environments.

Bittacus sylvaticus somewhat resembles *B. banksi* Esben Petersen in the lateral aspect of the epiandrial appendages and length of cerci. In *banksi*, however, the epiandrial appendages are not twisted or rotated near mid-length. The many spots on the wings of *sylvaticus* give it an almost mottled appearance not seen in any other Mexican species, although there are Mexican species of *Bittacus* with dark (but uniformly smoky) wings. In wing maculation and generally dark coloration, *B. sylvaticus* resembles *B. maculosus* Byers of Trinidad; however, the male of that species, described later in this paper, has quite different structure of the ter-

minal abdominal segments. The membranous medial separation of sterna 8 and 9 resembles the condition in *B. disternum* although it is much less extensive.

Bittacus spatulatus new species

Description based on 21 males and 32 females, pinned, and two males in alcohol. Additional specimens have been examined, but their condition is so poor that they are not included as paratypes.

Head: Dorsum and frons sordid dark yellowish brown; ocellar triangle black; diameter of lateral ocelli about 1.3 times that of median ocellus. Rostrum dark amber-brown, subgenae darker brown; mouthparts amber-brown, terminal segment of maxillary palps paler than other segments. Antennal scape and pedicel yellowish brown to amber-brown; flagellum blackish brown, with 21-22 flagellomeres, indistinct beyond 13.

Thorax: Pronotum sordid yellowish brown, with three transverse ridges, anterior one thickest and most elevated, with two large, black setae at each side, one dorsolateral, one lateral; posterior ridge with two shorter black setae at each side above anterior spiracle; posterior edge of pronotum curving around spiracle and converging with anterior edge so each side of pronotum terminates laterally in a sharply acute angle. Mesonotum unevenly dark yellowish brown except scutellum somewhat paler (much variation in shades of color apparently due to post-mortem changes); mesoscutum with conspicuously raised oblong area above and before each wing attachment; scutum with fine, pale, very short hairs, longer ones on scutellum slender, brown. Metanotum dark yellowish brown except scutellum slightly paler than scutum; hairs as on mesonotum. Pleural surfaces, coxae and mera unevenly brown with scattered yellow hairs, most dense on anterior surfaces of coxae, and fine, pale pubescence; two black setae vertically aligned on mesothoracic anepisternum, one or two on epimeron, two on metepimeron, 2 on fore coxa and 2-5 on hind coxa. Femora and tibiae yellowish brown, narrowly darkened with brown to blackish brown at apex, with black setae. Fore and middle tarsi yellowish brown, hind tarsus reddish brown; basitarsus of fore leg longer than tarsomeres 2-5 together, that of middle tarsus shorter than 2-5; hind basitarsus about one-third length of tarsomeres 2-5 together.

Wings slightly iridescent, strongly tinged with yellowish brown, without markings; stigma yellowish brown, veins dark yellowish brown to reddish brown; two stigmal cross-veins. Scv about midway between ORs and FRs; apical cross-vein present near end of 1A, before level of FRs. Five or six conspicuous black setae on both costal and hind margins of fore and hind wings between base and end of 2A. Inconspicuous pale thyridium at FM.

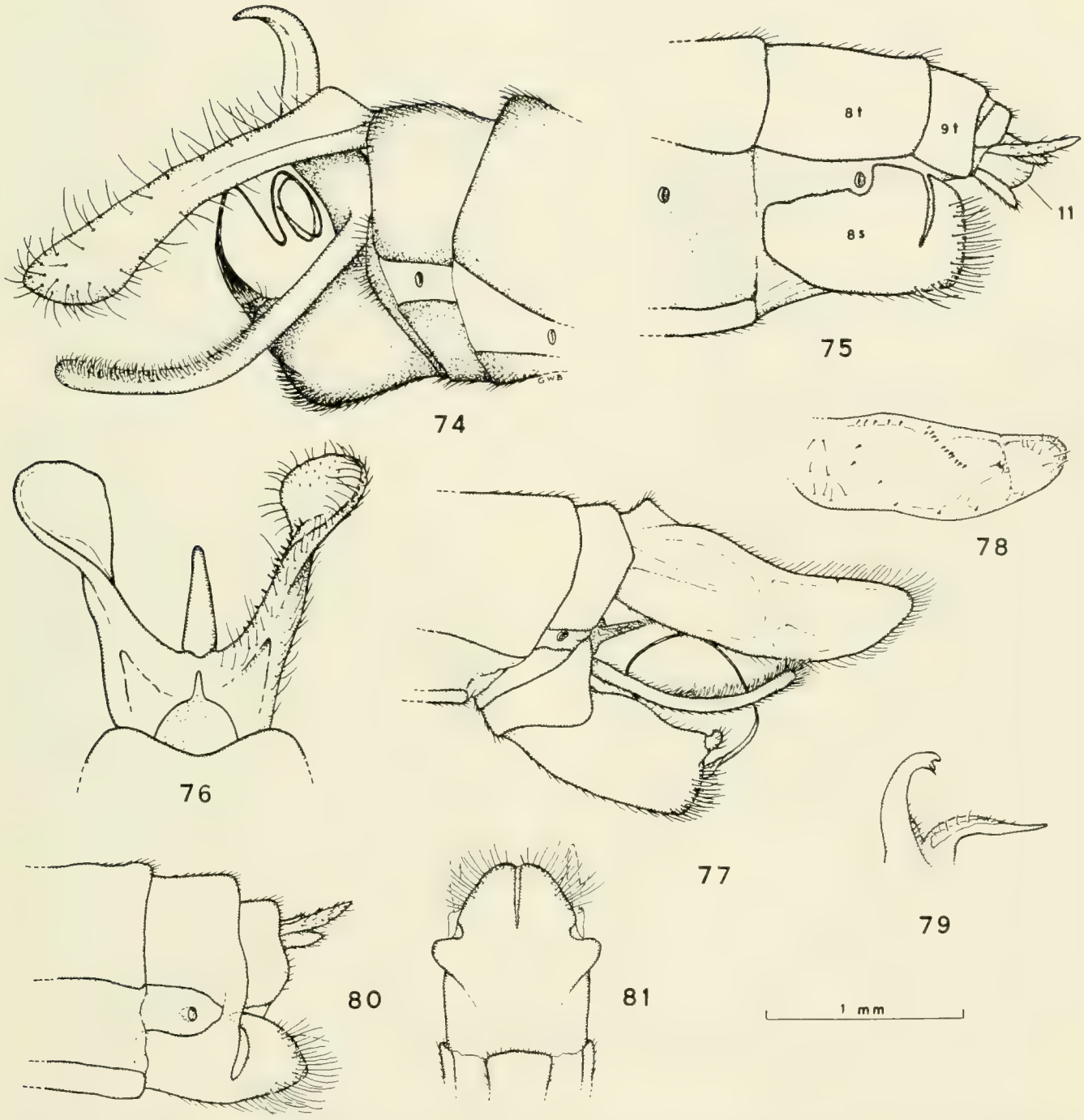
Abdomen of male: Terga 2-8 unevenly yellowish brown to sordid yellowish brown, with abundant short, yellow hairs; corresponding sterna slightly paler; sterna 3-6 long and narrow, usually drawn up beneath terga and largely concealed in dried specimens. Lateral margins of tergum 2 with usually 7-8 (range 7-12) conspicuous black setae on each side; tergum 3 with 7-14 shorter black setae on each side, fewer (1-6) on sides of terga 4 and 5. Tergum 8 broadly emarginate posterodorsally (Fig. 76). Epiandrial appendages (Figs. 74, 76) yellowish brown, much longer than basistyles, divergent (but not always as much as in Fig. 76), narrowest near mid-length and twisted so that mesal surfaces face dorsad or nearly so. Row of short, stout, recurved black spines along inner, dorsal edge of each epiandrial appendage, extending from near base to approximately mid-length, then turning diagonally ventrad to about mid-width of appendage. Small group of similar spines near ventral edge, near base of appendage. Apical half of each appendage expanded, somewhat concave and glabrous on upper (mesal) surface, with rounded posterior edge; glabrous, glossy surface bordered dorsally, ventrally and posteriorly by long, inwardly (or dorsally) directed setae; other long setae nearly perpendicular to margins. Basistyles only about half as long as epiandrial appendages, yellowish brown with yellow hairs; dististyles short, inwardly curved, narrowed subapically, apex strongly sclerotized. Cerci long, extending nearly to ends of epiandrial appendages, with dense yellow hairs, those along entire dorsal surface suberect, slightly recurved. Aedeagus subconical near base, filamentous for most of its length (first coil often adhered to lower branch of proctiger, in dried specimens, and subsequent coils adhered to walls or floor of genital chamber). Upper branch of proctiger glabrous, arched upward between bases of epiandrial appendages; lower branch long-triangular with few bordering setae.

Abdomen of female: Sordid yellowish brown to dark brown with abundant short, yellow hairs; specimens containing numerous eggs darker than those that had laid most eggs. Sternum 8 and subgenital plate broadly joined (Fig. 75) but partially separated by deep, narrow notch in dorsal margin; membranous ventral separation wide anteriorly between sclerites of sternum 8, converging to narrow separation of subgenital plates. Sternum 8 curved around spiracle posteriorly; subgenital plate truncate posteriorly, with long setae, some slightly upturned. Segments 10 and 11 withdrawn under tergum 9, cerci partially visible, in dried specimens (cf. Fig. 75). Eggs cuboidal with surfaces impressed.

Measurements: Body length, male, about 20.7-23.2 mm (holotype 23.1 mm); female, about 18.0-20.4 mm (allotype 20.4 mm). Length of fore wing, male, 20.3-24.2 mm (holotype 24.0 mm); female, 20.6-23.5 mm (allotype 22.1 mm). Antennal length, male, about 9.2-10.8 mm (holotype 10.0 mm); female 9.1-10.3 mm (allotype 10.3 mm).

Types: Holotype, male, allotype female, 3 male and 6 female paratypes collected near Taboga (14 miles SW of Cañas), Guanacaste Prov., Costa Rica, 25-26 July 1967, by Oliver S. Flint, Jr. Additional paratypes: COSTA RICA: Guanacaste, Bagaces, Río Piedras, 27 July 1967 (1 male, 3 females); Guanacaste, 1.5 mi. S of Potrerillos, 27 July 1967 (1 female); Guanacaste, Las Cañas vicinity, Río Corobicí, 26 July 1967 (3 males); all these localities are on the Interamerican Highway, all specimens collected by O. S. Flint, Jr. (USNM, SEM). Guanacaste, 14 km south of Cañas, at flight-intercept trap, 3-9 July 1988 (1 male), 1-4 Sept. 1989 (1 female), 15-22 Jan. 1990 (1 male), 29 July 1990 (1 female), 1-12 Aug. 1990 (1 male, 1 female), 14-17 Aug. 1990 (1 male), 16-19 Sept. 1990 (1 male), 1-22 June 1991 (2 males, 2 females), 22-30 June 1991 (1 male, 2 females), 1-10 July 1991 (1 male, 1 female), all collected by Frank D. Parker (USU, SEM). Guanacaste, Palo Verde, 5 July 1976, Robert Gorton (1 male; USNM); S. Cañas Exp. Sta., 1-8 August 1988, F. D. Parker (2 males, 1 female; USU). Puntarenas, Playa Naranjo, 19 July 1975, L. F. Jiron (1 male). NICARAGUA: Chontales, 4 miles NW of Acoyapa, 29 July 1967, O. S. Flint, Jr. (1 female; USNM); Masaya, Las Flores, June 1987, at uv. light, J.-M. Maes (1 male); Leon vicinity, Lake Telica, July 1990, B. Garcete (2 males); Masaya, Las Flores, in Malaise trap, 1 July 1994 (1 male), 8 July 1994 (1 male, 4 females), 27 July 1994 (2 females), all collected by Jean-Michael Maes (MELN). Holotype, allotype and paratypes as indicated in the USNM; paratypes in SEM and other collections as indicated.

Bittacus spatulatus closely resembles *B. banksi* Esben-Petersen in size and in venation and coloration of wings, and its known range falls completely within that of *banksi* (Mexico to Panama). Differentiation of females of these two species is particularly difficult. Males of *B. spatulatus* can be recognized by the peculiar rotation and subapical widening of the epiandrial appendages. It is this characteristic combined with the shallowly concave, upturned mesal surface that gives the species its name (Latin *spatula* = diminutive form for a broad, flat spoon or stirring tool). The distal one-third of an epiandrial appendage in *B. banksi*, while somewhat widened, is not particularly concave on the mesal surface, and the epiandrial appendages are ordinarily held close together (subparallel), not divergent as in *spatulatus*. In males of *B. spatulatus* from near Cañas, Guanacaste, Costa



Figs. 74-76. *Bittacus spatulatus* n. sp. 74, terminal abdominal segments, male paratype, right lateral aspect. 75, terminal abdominal segments, female paratype, left lateral aspect; s - sternum, t - tergum, eleventh segment indicated. 76, epiandrial appendages and proctiger, dorsal aspect. **Figs. 77-81.** *Bittacus peninsularis* n. sp. 77, terminal abdominal segments, male holotype, left lateral aspect. 78, mesal aspect of right epiandrial appendage to show distribution of spines, hairs and ridges. 79, proctiger of male, left lateral aspect. 80, terminal abdominal segments, female paratype, left lateral aspect. 81, same, ventral aspect, showing undivided eighth sternum. Scale, all figures.

Rica, the ratio of greatest width of the apical one-third to the narrowest near mid-length of an epiandrial appendage, seen in lateral profile, is 1.87-2.0 to 1, while in *B. banksi* from the same locality it is only 1.17 to 1. Less conspicuous rotation of the epiandrial appendages is seen in *B. sylvaticus,* a Mexican species that can be recognized by its darkly marked wings and quite differently shaped epiandrial appendages (compare Figs. 76 and 73). Females of *B. spatulatus* have the posterior edge of the subgenital plate (on each side) nearly vertical, or truncate; however, in dried specimens there is often enough deformity to make this difficult to see.

Bittacus peninsularis new species

Description based on 27 males, 23 females, pinned; 18 additional females seen but not made paratypes because of poor condition.

Head: Dorsum unevenly brown to dark brown; ocellar prominence black; ocelli strongly protruding, lateral ocelli longer than high, greatest length 1.45-1.75 times that of median ocellus; frons deeply recessed below median ocellus and between antennal bases. Rostrum dark amber brown near base darkening toward apex; prominent subgenal ridge at each side of clypeus below eye; mouthparts amber-brown, maxillary palps black. Antennal scape and pedicel sordid brown, flagellum black, with 21-23 flagellomeres (indistinct beyond 14), hairs on flagellomeres beyond third longer than diameter of flagellomere, increasingly so distally.

Thorax: Pronotum sordid yellowish brown; 4-6 conspicuous black setae on anterior margin, one dorsolateral, one or two more lateral, on each side, each on slight elevation; two setae on posterior margin; anterior spiracle appressed to posterior margin on each side. Mesonotum and metanotum unevenly dark yellowish brown with numerous short, yellowish hairs; conspicuous black seta at each side on mesonotal prominence above and before wing attachment; two smaller black setae on mesonotal scutellum. Pleural surfaces, coxae and mera unevenly brown with fine whitish pubescence and scattered yellow hairs, latter most dense on coxae; 1-2 large black setae on mesothoracic anepisternum, 1-2 on meso- and metathoracic anepimera, 2-4 in vertical alignment on hind coxa. Femora and tibiae dark yellowish brown to amber-colored, narrowly darkened at apex; four uneven rows of long, black setae along dorsum and sides of hind femur. Tarsi only slightly darker than legs; fore and middle basitarsi subequal in length to tarsomeres 2-5 together; hind tarsi thicker than others, basitarsus about two-thirds as long as fore basitarsus.

Wings strongly tinged throughout with dark yellowish brown, slightly darker around apical margin, somewhat iridescent; stigma scarcely darker than adjacent wing membrane; veins brown to amber-brown; two pterostigmal cross-veins. On posterior margin of fore wing and on both costal and hind margins of hind wing, 4-5 conspicuous black setae between wing base and level of end of vein 2A. Sc joins C beyond FRs; Scv about half-way between ORs and FRs; no apical cross-vein between Cu2 and 1A. Pale (not whitish) thyridium at FM.

Abdomen of male: Terga yellowish brown (terga 2-5 of holotype) to sordid dark yellowish brown, with abundant short, yellowish hairs; sterna slightly paler, those of segments 2-6 usually drawn upward and concealed by terga in dried specimens; 7-9 black setae along each side of combined terga 1-2, 7 on each side of tergum 3, 4 on tergum 4, 0-2 on tergum 5. Epiandrial appendages (Fig. 77) unevenly yellowish brown, slightly darker near apex, extending well beyond ends of basistyles, with thickened margins and pale ridge at mid-width from base to one-fourth to half length of appendage. Three or four short black spines along inner, dorsal edge of appendage (Fig. 78), about 12 on diagonal ridge on mesal surface between dorsal margin and mid-width, ridge increasing in height (thickness) toward lower, caudal end; two larger black setae on small prominence farther caudad; scattered hairs on inner surface of appendage near apex and hairs and spines elsewhere, as illustrated. Basistyles about twice as long as high, with long setae on posterior surface; dististyles small, simple, incurved to rounded apex. Aedeagus only slightly enlarged near base, mostly finely filiform, with more than three full coils (usually adhered to wall of genital chamber and not seen in dried individuals). Cerci longer than basistyles, shorter than epiandrial appendages, with long, slightly recurved hairs on dorsal surface of distal half and dense tuft of long hairs at apex. Dorsal branch of proctiger (Fig. 79) arched upward and backward to bifurcate tip, largely glabrous except along ventrolateral margins; lower branch tapering to acute apex, with few long setae along each side.

Abdomen of female: Terga and sterna unevenly yellowish brown, as in male. Eighth tergum and sternum joined by lightly to moderately sclerotized (not membranous) band behind spiracle (Fig. 80); area of fusion protruding to side in ventral aspect (Fig. 81); sternum 8 not divided ventrally, with median band of short, yellow hairs; subgenital plates separated by narrow, mid-ventral membranous zone. Subgenital plates rounded posteriorly, with long setae; anterodorsal tip of each inserted beneath sclerotized bridge between eighth tergum and sternum.

Measurements: Body length, male, about 15.5-17.5 mm (holotype 17.2 mm); female, about 13.8-16.6 mm (allotype 15.6 mm). Length of fore wing, male, 18.2-20.0 mm (holotype 20.0 mm); female, 17.0-19.8 mm (allotype 19.0 mm). Antennal length, male, about 9.5 mm, female about 8.2 mm.

Types: Holotype, male, allotype and 5 male, 9 female paratypes collected at black (ultraviolet) light, at Ramal de Naranjas, 6 miles west of Highway 1 near Santa Anita, Baja California Sur, Mexico, on 11 October 1983, by F. G. Andrews and D. K. Faulkner. Holotype, allotype and most paratypes in SDM; 3 male, 1 female paratypes in SEM. Additional paratypes, all from Baja California Sur: El Salto, 8 miles northeast of Todos Santos, at black light, 9 Oct. 1983, Andrews and Faulkner (5 males, 7 females; SDM, SEM); 36.6 miles southeast of Todos Santos, 10 Oct. 1983, Faulkner and Andrews (3 males, 2 females; SDM); Sierra de la Laguna, road to San Antonio de la Sierra, 8.5 road miles S and E of Highway 1 (KP#148), 2400 ft., 8 Sept. 1984 (no. 88,433), J. P. and K. E. Donahue (1 male, 1 female; LACM); same general locality but 1.7 road miles from Hwy. 1, 1500 ft., 12 Sept. 1984 (no. 88,574) (1 male, 1 female; LACM); Rancho la Burrera, 1800 ft., 6 Oct. 1975, R. R. Snelling (8 males, 1 female; LACM, SEM); 3 miles southwest of San Antonio, 14 Oct. 1972, E. M. and J. L. Fisher (1 male; SEM); Cañon de la Zorra, 6 miles west of Santiago, 1000 ft., 16 Oct. 1972, D. C. Marqua (1 male, 1 female; SEM).

Bittacus peninsularis resembles *B. texanus* Banks in numerous details of color and structure and will be identified as that species in existing keys. Seeing specimens of both species side by side, one notices the smaller size of *B. peninsularis* (its largest individuals approximately the size of the smaller ones of *B. texanus*) and its somewhat paler wings. The ranges of these two species are separated by over 1500 km (about 940 miles), but the ranges of both are only poorly known. Males of *peninsularis* can rather readily be differentiated from those of *texanus* by the epiandrial appendages, which are shorter and wider in *peninsularis;* this can be stated as a ratio of total length of the appendage to its width at mid-length, which is 3.35 in *peninsularis* and 4.40 in *texanus.* The diagonal ridge on the inner surface of the epiandrial appendage in *peninsularis* is not present in *texanus* but is probably represented by a prominence near the dorsal edge bearing a few black spines; and in *texanus* there are several more spines (number varies) along the inner dorsal margin of the appendage between its base and mid-length. Females of *texanus* have, on each side of tergum 8,

a prolongation downward behind the spiracle, into the notch between sternum 8 and the subgenital plate, but the connection of tergum and sternum is not complete as it is in *peninsularis*.

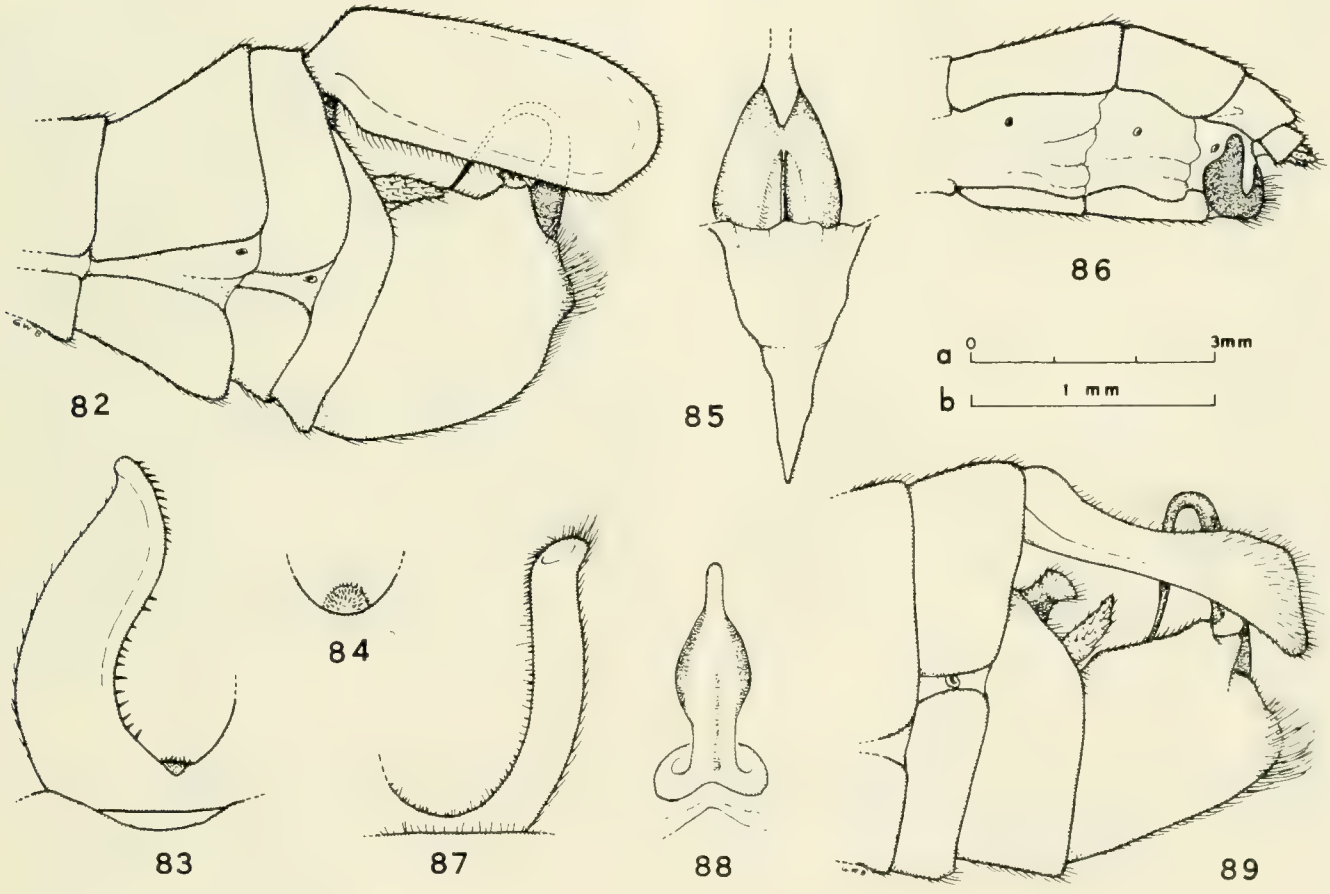
In a letter, Dr. Faulkner described the habitats at the sites of his collections as having lush thorn scrub vegetation with occasional oaks and palms, the ground dry, however, as there had been no rain for several days. Bittacids taken at light on 9 October were catching and feeding on small Lepidoptera; one paratype is pinned together with its prey, a small moth.

The species takes its name from its occurrence at the southern end of the peninsula of Baja California.

Bittacus pignatellii Navás

Although this is a large bittacid, of striking appearance because of its size, its black-tipped femora and tibiae and its maculate wings, and although it lives in an area where there has been extensive insect collecting, a second specimen was not found until 50 years after publication of the original description (Navás, 1932). The female holotype was collected at Punta de Sabana, Darién, in eastern Panama. The second female was found near Santa Clara, Chiriquí, at an elevation of 1200 m, in western Panama, 22-25 May 1982, by Brett C. Ratcliffe, who donated it to the Snow Entomological Museum. More recently, the first known male of this species was collected at a mercury vapor light operated at Quebrada Juan Grande, km 2 on Pipeline Road, former Panama Canal Zone, on 9 June 1993, by Steven W. Lingafelter of the Snow Museum.

Navás' description of *Bittacus pignatellii* dealt largely with color. Some structural characteristics of the holotype deserve mention, including: Diameter of lateral ocelli twice that of median ocellus. Antennae with approximately 19 flagellomeres (not distinct beyond 15th). Pronotum with



Figs. 82-86. *Bittacus pignatellii* Navás. 82, terminal abdominal segments of male, left lateral aspect. 83, right epiandrial appendage (and part of left one) with spinose lobe at base partially visible. 84, spinose median lobe at base of epiandrial appendages, posterodorsal aspect. 85, base of aedeagus and membranous median separation of basistyles, posterior aspect. 86, terminal abdominal segments (6-11) of female holotype, left lateral aspect. **Figs. 87-89.** *Bittacus maculosus* Byers. 87, left epiandrial appendage of male, dorsal aspect. 88, base of aedeagus, posterior aspect. 89, terminal abdominal segments of male, left lateral aspect. Scale a, fig. 86; scale b, figs. 82-84, 87-89.

two large black setae on anterior margin and two on posterior margin. Thoracic pleura with silvery pubescence. Eighth abdominal sternum (Fig. 86) darkly sclerotized, with lateral extension behind spiracle at each side and with broad attachment to nearly vertically-oriented, setose subgenital plate; halves of subgenital plate very narrowly separated along ventral midline.

All the wings of the holotype are somewhat tattered, but I was able to make a restoration of the right fore wing (Fig. 90) by reference to the others. The wings are tinged with yellowish brown, the markings dark brown, the stigma particularly dark and elongate. Vein R_{2+3} turns abruptly from R_{4+5}; and there is a conspicuous thyridium at the first fork of the media. I am grateful to Dr. P. Passerin d'Entreves, curator of insects in the Museo ed Instituto di Zoologia Sistematica, Università di Torino, Italy, for the loan of the holotype specimen.

The terminal abdominal segments of the male (Figs. 82-84) are characterized by thick basistyles deeply separated posteroventrally by a triangular membranous area (Fig. 85), and by outwardly convex epiandrial lobes sparsely covered with short hairs (Fig. 83) and bearing black spines on the dorsomesal margin. At the anterior separation of the epiandrial lobes, scarcely visible in dorsal aspect, is a low, rounded lobe bearing numerous black spines (Figs. 83, 84). The base of the aedeagus, in ventral aspect (Fig. 85), is glossy and dark brown with two subtriangular impressed areas separated by a median carina.

Bittacus maculosus Byers

The original description (Byers, 1965) was based on one female, collected at light at St. Augustine, Trinidad (type in the USNM), and a second female was taken in Manaus, Brasil (Penny and Arias, 1982). Only recently the first male has been found. This male was collected at an ultraviolet light in wet forest just above St. Augustine, Trinidad (10°39'N, 61°24'W), near Mount St. Benedict Stream, 250 m elevation, 20-25 June 1993, by Nancy E. Adams. I am indebted to Dr. Oliver S. Flint, Jr., of the National Museum of Natural History for sending me this specimen for examination.

In color characteristics, the male is much the same as the female holotype, allowance being made for slight postmortem changes in the color of thorax and abdomen in particular, in the two specimens. The second flagellomere of the male is apically darkened, like those beyond it, while the first two are pale in the female. Also there are some small differences in wing maculation.

The terminal abdominal segments of the male are distinctive: Epiandrial appendages slender, in lateral aspect somewhat narrowed near mid-length, then expanded apically, with a shallow apical depression (Figs. 87, 89). Numerous short, black spines along inner, dorsal margin of each lobe, those toward apex longer and more dense than those nearer base. Aedeagus thick near its base in lateral aspect (Fig. 89), relatively short and not coiled; in posterior aspect (Fig. 88) widened laterally beyond base, sides very darkly sclerotized. Dististyle hairy on outer curvature, with sharp, densely sclerotized, subapical point on inner surface. Proctiger short, of simple structure; cerci short, thick.

Kalobittacus maniculatus new species

Description based on two males, four females, pinned.

Head: Dorsum dark yellowish brown except piceous around ocelli and brown band extending from eye to eye, arching above antennal sockets and including ocellar prominence. Frons below antennal bases and rostrum yellowish brown; subgenae slightly darker, maxillae dark amber-brown, maxillary palps yellowish brown. Antennal scape and pedicel light yellowish brown, flagellum gradually darkening toward tip; about 21 flagellomeres (indistinct beyond 14th); flagellar hairs longer than diameter of flagellomeres.

Thorax: Anterior propleura large, their posterior edges inserted beneath pronotum; setae yellow. Pronotum yellowish brown; anterior margin a rounded, transverse ridge somewhat expanded at sides; one or two black setae on each posterolateral corner above spiracle. Mesonotum, metanotum, pleural surfaces, coxae and mera unevenly yellowish brown. Pleura and coxae with scattered yellowish hairs, most numerous and longest on coxae; posterodorsal edges of mesothoracic and metathoracic mera narrowly black. Femora and tibiae yellowish brown to amber-brown, with black setae in poorly defined rows; hind femora of males slightly incrassate near mid-length. Fore and middle tarsi yellowish brown, with basitarsus as long as tarsomeres 2-5 together; hind tarsi darker brown, thicker, with shorter basitarsus.

Wings (Fig. 99c) faintly tinged with yellowish brown, hyaline, highly iridescent; stigma and apical spot dark brown. Stigma extending from costa to R_{2+3}; two stigmal cross-veins. In fore wing, subcostal cross-vein near level of FRs, 1A ending at posterior margin at level of OM, vein 2A about half as long as 1A; cross-vein from 1A to posterior margin at or slightly beyond end of 2A. In hind wing, 1A fused with Cu_2 to level of OM, turning as diagonal cross-

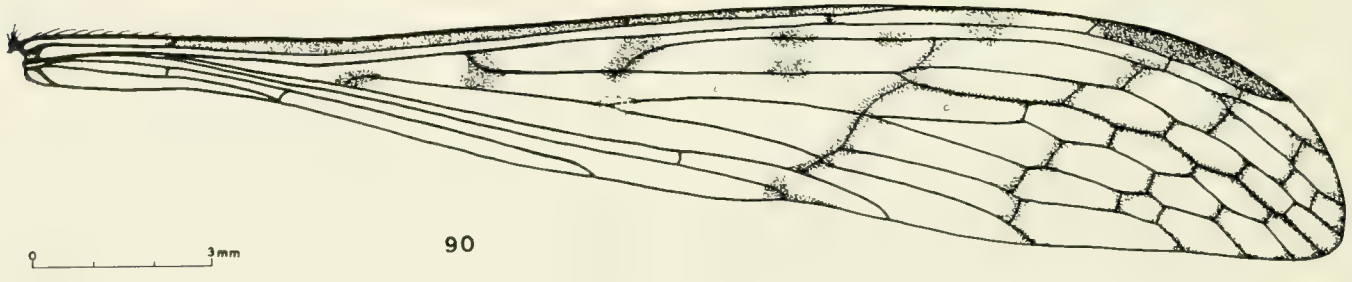


Fig. 90. *Bittacus pignatellii* Navás, right fore wing (composite drawing from all wings of female holotype).

vein to wing margin; 2A ending at level of humeral cross-vein, near wing base. Pale thyridium at first fork of M; nygmata between R_{4+5} and M_{1+2} and between R_5 and M_1 where veins are closest together. Four black setae along costa of fore wing between base and level of end of 1A; two similar but longer setae on anal lobe of wing; four or five long, black setae on proximal costa of hind wing, similar number on posterior edge near wing base.

Abdomen of male: Terga 2-5 yellowish brown, with 4 conspicuous black setae on each lateral margin of tergum 2, 1 or 2 on sides of terga 3-5; corresponding sterna yellowish brown, narrow, deeply recessed beneath terga in dried specimens. Terga 6-8 conspicuously darker, blackish brown; tergum 6 about 0.6 as long as tergum 5, its posterior end 1.6 times as wide as anterior end; tergum 7 about 0.7 times length of 6, widening to 1.25 times its anterior width; tergum 8 short, wide, with broadly U-shaped posteromedian emargination. Epiandrial appendages (Figs. 91, 92) unevenly yellowish brown, gradually downcurved, about 1.7 times length of basistyles., with conspicuous thumb-like lobe on dorsal margin directed dorsad and mesad and bearing small group of short, black spines at apex, 0-3 others before apex on underside. Most setae on outer surfaces of epiandrial lobes slender and yellow; thicker, longer, black setae at apex and a few along subapical, ventral margin. Spine-tipped subconical lobe on inner surface of each epiandrial lobe near base; smaller lobe with only one terminal spine near lower mesal margin at level of "thumb." Sterna 8 and 9 and basistyles blackish brown except basistyles dark brown apically. Dististyles short, simple, curved inward. Aedeagus thick at base, with lateral expansions (penunci), then elongate but not coiled, ending near proctiger. Proctiger branched, upper branch reaching dorsal margins of epiandrial lobes at their divergence; lower branch short. Cerci yellowish, acutely tipped, not reaching ends of basistyles.

Abdomen of female: Terga 2-4 yellowish brown, 5 slightly darker, 6-7 dark yellowish brown dorsally, blackish brown at sides; sterna 2-5 narrow, yellowish brown, 6-7 widening backward, dark brown. Tergum and sternum of segment 8 fused, pleura sclerotized (Fig. 93), glossy dark brown dorsally and ventrally, black at sides (and across anterior dorsum in one female) except pale around protruding spiracle; fused sclerites forming nearly complete ring, ventral edges narrowly separated by membrane. Anterior margin of segment 8 thickened on each side and protruding laterally as two rounded prominences. Subgenital plates dark yellowish brown with long apical hairs; narrowly separated ventrally by membrane.

Measurements: Body length, male, about 16.0-16.3 mm (holotype 16.3 mm); female, about 14.9-15.5 mm (allotype 14.9 mm). Length of fore wing, male, 17.0-17.8 mm (holotype 17.0 mm); female, 17.4-17.8 mm (allotype 17.4 mm. Antennal length, male and female, about 4.5-5.0 mm.

Types: Holotype, male, allotype, female, 1 male and 3 female paratypes collected 20 miles (32 km) northwest of Huehuetenango, Guatemala, 9-10 August 1967, by O. S. Flint, Jr. Holotype, allotype and 3 female paratypes in the USNM, male paratype in the SEM.

A few characteristics of *K. maniculatus* set this species quite apart from all known congeners. For example, the thumb-like process on the epiandrial lobe of the male and the fusion of the eighth tergum and sternum with lateral projections in the female are without equivalents in any other known species of *Kalobittacus*. In body color and wing maculation, *maniculatus* resembles *K. hubbelli* Byers of Honduras and *K. masoni* Byers of southern Mexico. The long epiandrial lobes somewhat resemble those of *hubbelli* and *masoni* but are curved downward instead of upward and are not narrowly rounded apically as in those species.

The name *maniculatus* refers to the "thumb" and general shape of the epiandrial lobes (Latin *maniculatus* = with or having little hands).

Kalobittacus inornatus new species

Description based on one male preserved in alcohol; described patterns of color are probably reliable, while colors may vary from those of dried specimens or the living insects.

Head: Occiput and vertex behind ocelli light brown; anterior vertex brown from eye to eye; ocelli narrowly bordered with black; lateral ocelli approximately same diameter as median ocellus. Frons below antennal sockets brown; clypeus light brown, remainder of rostrum and mouthparts, including maxillary palps, yellowish brown. Antennal scape and pedicel light gray; flagellum pale yellowish brown with about 20 flagellomeres (long, with indistinct ends beyond eighth except terminal flagellomere short); hairs longer than diameter of flagellomeres in distal half of antennae.

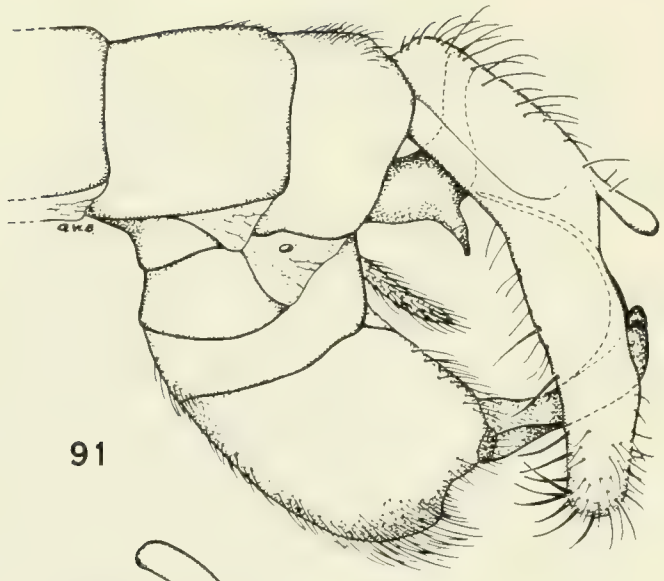
Thorax: Pronotum brown, its anterior margin thickened and rounded as transverse ridge, without setae; posterior pronotum separated from anterior margin by deep transverse sulcus. Anterior spiracles large, their length greater than width of adjacent part of pronotum. Mesonotum brown anteriorly, slightly darker brown posteriorly, with intervening depressed area pale brown; scutellum pale gray (nearly white); few pale hairs on posteriormost scutum, two longer pale setae on scutellum. Metanotum similar to mesonotum except pale transverse area diffuse and indistinct. Propleura brown, inserted posteriorly beneath pronotum, but pleural suture visible; front of anterior coxae light brown, posterior half pale gray. Mesepisternum light brown, with one black seta and small group of short hairs on anepisternum below attachment of fore wing; mesepimeron and respective meron and coxa pale gray; metepisternum and coxa only, slightly darker than pale gray metepimerion and meron, anepisternum with few pale hairs. Femora pale near base, mostly dark yellowish brown, apex narrowly black; hind femora nearly twice diameter of middle femora throughout but not incrassate in appearance; tibiae dark yellowish brown, narrowly black at apex; anterior and middle tarsi yellowish brown, their basitarsi as long as tarsomeres 2-5 together; hind tarsi thicker, darker, with basitarsi only about half as long as those of other tarsi.

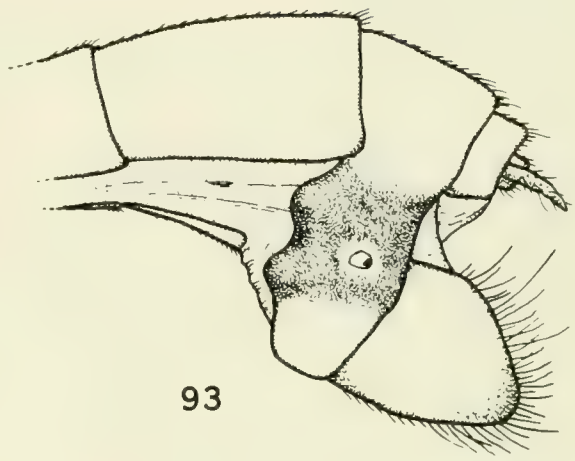
Wings hyaline, highly iridescent, faintly tinged with yellowish brown; stigma light yellowish brown, enclosing two pterostigmal cross-veins; faint, diffuse yellowish brown clouding at ORs, FRs and OM. No apical spot. Vein 1A joining hind margin of wing slightly beyond level of OM in fore wing, fused with Cu_2 for most of its length in hind wing and crossing to margin as long-diagonal cross-vein.

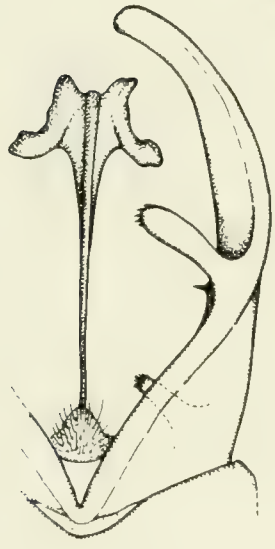
Abdomen of male: Terga 2-6 light brown, 7 brown anteriorly except for narrow, black anterior edge, grading into yellowish brown posteriorly; tergum 8 brown with narrow, black anterior edge; sterna paler than corresponding terga. Caudal edge of tergum 8 broadly and shallowly emarginate. Epiandrial lobes (Figs. 94, 95) basally grayish brown with mixed pale and dark hairs, pale yellowish brown with mostly yellowish hairs in distal one-third; two or three black spines on inner caudal edge; tuft of hairs and single black spine on mesal surface slightly behind mid-length; low prominence nearer base with numerous small, black apical spines; sternum 9 pale laterally, brown ventrally. Basistyles brown; dististyles brown, simple, strongly curved inward, with abundant dark hairs. Aedeagus widened near base, its slender, brown median tube with pale brownish gray supporting structures along each side and tapering toward mid-length; apical half filiform, terminating near aedeagal base (i.e., nearly one full coil); brown swelling at each side near base. Cerci of medium length with acute apex and abundant setae. Proctiger pale gray near base, dorsal branch light yellowish brown, with yellowish hairs along sides; ventral branch pale with marginal hairs; separation of branches directed dorsad (Fig. 95).

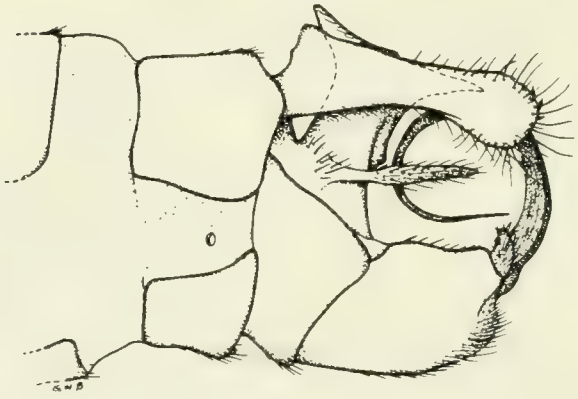
Measurements: Body length, male, about 16 mm. Length of fore wing, male holotype, 17.8 mm. Length of antenna about 4.9 mm.

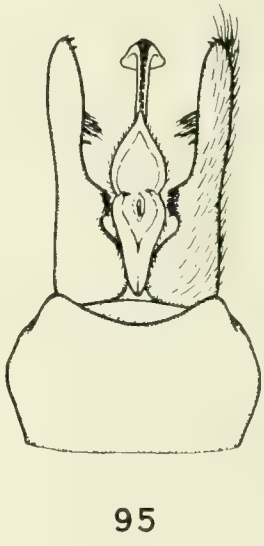
Type: Holotype, male, collected 6 km south of San Vito (southeasternmost Puntarenas Prov.), Costa Rica, 3 May 1967, by Donald F. Veirs; in the SEM.

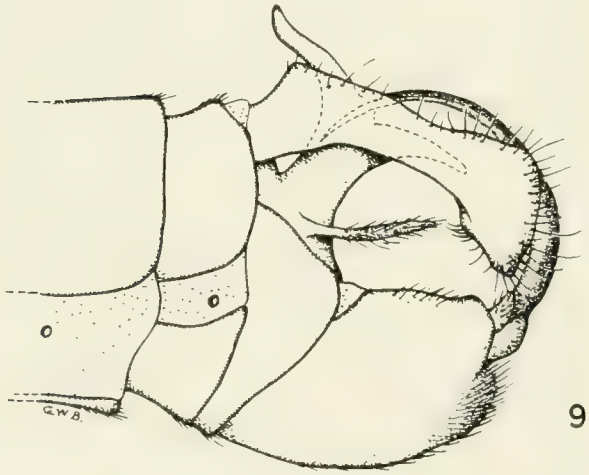


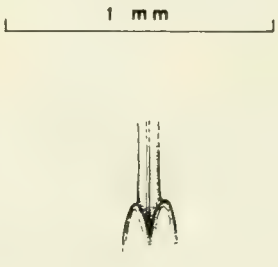


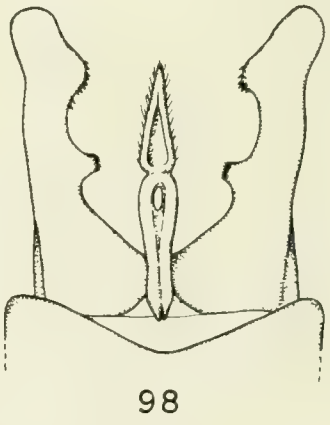












Figs. 91-93. *Kalobittacus maculatus* n. sp. 91, terminal abdominal segments, male holotype, left lateral aspect. 92, left epiandrial appendage and aedeagus, dorsal aspect. 93, terminal abdominal segments of female, left lateral aspect. **Figs. 94-95.** *Kalobittacus ornatus* n. sp., male holotype. 94, terminal abdominal segments, left lateral aspect. 95, epiandrial appendages, proctiger, aedeagus and eighth abdominal tergum, dorsal aspect. **Figs. 96-98.** *Kalobittacus demissus* n. sp., male holotype. 96, terminal abdominal segments, left lateral aspect. 97, base of aedeagus, posterior aspect. 98, epiandrial appendages and proctiger, dorsal aspect. Scale, figs. 91-96, 98.

The male of *Kalobittacus inornatus* has several similarities to males of *K. demissus,* such as the large proctiger with a virtually dorsal opening and the two branches turned in nearly opposite directions, the simple aedeagus without a complete coil, and the low, spinose projection on the dorsal edge of each epiandrial lobe. In being narrowed near mid-length and enlarged in the apical one-third, the epiandrial lobes of these two species show a general similarity, while these structures differ conspicuously in detail (compare Figs. 94, 96) and at the same time set *inornatus* and *demissus* apart from all other known species of *Kalobittacus.* It is the simple form of the epiandrial lobes, simple aedeagus and wings without conspicuous pterostigma or apical spot that suggest the name *inornatus* (Latin, simple, unadorned).

Kalobittacus demissus new species

Description based on two males preserved in alcohol; described color patterns are probably reliable, but described colors may not be accurate for dried specimens or the live insects.

Head: Dorsum brown to blackish brown, black around ocelli; greatest width of lateral ocellus about 1.9 times diameter of median ocellus; frons dark brown, rostrum dark brown near base, unevenly amber-brown apically; mouthparts amber-brown, maxillary palps dark yellowish brown to brown. Antennal scape and pedicel sordid yellowish brown to brown, flagellum yellowish brown to light grayish brown, with 17-18 flagellomeres (indistinct beyond 11 or 12), apical one-third of terminal flagellomere black; hairs longer than diameter of outer flagellomeres.

Thorax: Anterior propleura conspicuous, oval, with pale marginal hairs; posterior edges inserted beneath pronotum. Pronotum brown, its anterior margin thickened and rounded, without setae; posterior margin thin, without setae. Mesonotum and metanotum light brown anteriorly and along median depression, slightly darker on elevated areas, with brown spot at each side just anterior to pale scutellum and diffuse brown spot near each wing base; no setae. Pleura, coxae and mera unevenly light grayish brown, with diffuse brown on anterior mesothoracic coxae and episterna; hairs fine, short and sparse. Femora brown, slightly darkened apically, with black setae; hind femora thickened near mid-length to nearly twice diameter of either end, with conspicuous black setae in mesal, dorsal and lateral rows of three each on thickened part. Tibiae light brown, darkened apically, with sparse black setae. Tarsi dark yellowish brown; basitarsi of fore and middle legs subequal in length to tarsomeres 2-5 together; hind tarsi enlarged, basitarsi relatively shorter.

Wings highly iridescent, hyaline, very lightly tinged with yellowish brown especially along anterior edges; veins and markings brown to dark brown. Stigmal spot large, dark brown, mainly between C and R_{2+3}, enclosing two stigmal cross-veins. Apical spot brown, mostly in outermost cell R_4, with extensions into parts of apical cells R_3 and R_5; in fore wing, brown spots at ORs, FRs and OM mainly between R and M. Pale thyridium at FM, another, smaller one at base of M_4. Four conspicuous black setae on costa of fore wing before level of OM; two or three similar setae on posterior edge near base; 2-4 black setae on each edge of hind wing, nearer base. In hind wing, 1A coalesced with Cu_2 for most of its length, crossing to hind margin near level of OM.

Abdomen of male: Terga 2-6 unevenly dark yellowish brown, 2-3 with sparse black setae on lateral margins; corresponding sterna long-rectangular, paler than terga. Terga 7-8 shorter than more anterior ones, dark brown to black; posterior edge of tergum 8 broadly emarginate; sterna 7-8 also short and darkened (color contrast between segments 2-6 and 7-8 greater in holotype than in paratype). Epiandrial appendages (Figs. 96, 98) blackish brown in approximately basal half, grading into dark yellowish brown near apex (holotype) or in apical one-third (paratype), their dorsal and ventral edges nearly parallel in proximal 0.6, distal 0.4 widened, turned slightly outward but conspicuously downward, concave on inner or mesal surfaces, concavity surrounded by long yellowish hairs on dorsal, distal and ventral margins and by transverse ridge proximally; group of 6-11 short, black spines at upper end of ridge. On dorsal edge of each epiandrial lobe, near mid-length, a short, blunt, spinose projection directed mesad. Basistyles about as long as epiandrial lobes, dark brown with yellowish hairs; dististyles simple, small, inwardly curved. Aedeagus somewhat widened near base, with pair of rounded scales appressed to base posteriorly (Fig. 97), abruptly narrowed near mid-length, not coiled, terminating beside proctiger. Upper branch of proctiger curved cephalad between and above bases of epiandrial appendages; lower branch tapering, pale, with long setae. Cerci short, slender, acute at apex.

Measurements: Body length, male, about 15 to 17 mm (holotype 17 mm). Length of fore wing 16.5-18.0 mm (holotype 18.0 mm). Antennal length about 4.5 mm.

Types: Holotype, male, collected beside Interamerican Highway northwest of Esparta, northwestern Puntarenas Prov., Costa Rica, 8 August 1968, by Donald F. Veirs. One male paratype collected 4 miles (6.4 km) south of Rincón de Osa, Peninsula de Osa, southern Puntarenas Prov., Costa Rica, 3 May 1969, by Robin Andrews. Both specimens are in the SEM.

Kalobittacus demissus appears to be most closely related to *K. bimaculatus* Esben-Petersen and *K. similis* Byers, both of southern Mexico, on the basis of the structure of the epiandrial lobes, the aedeagus and the proctiger (cf. Byers, 1994: 1096, figs. 3-5). It most nearly resembles *bimaculatus* in wing markings. From both these species it differs most conspicuously in the apical portion of the epiandrial lobes; the posterior margin of these, in lateral profile, is concave in *bimaculatus* and *similis* but somewhat convex in *demissus.* While the dorsal edge of each lobe curves slightly upward to a posterodorsal point in the two Mexican species, it turns downward in *demissus* so that the widened apical part of the lobe appears to hang downward, hence the species' name (Latin *demissus* = hanging down, or drooping). The scale-like structures at the base of the aedeagus do not occur in *bimaculatus* or *similis;* and the proctiger in *demissus* is considerably larger than in those species, its branches separating more dorsally than in either *bimaculatus* or *similis.* And in *demissus* the apical wing spot is more restricted in extent than in *bimaculatus.*

No ecological data accompany either of the specimens of *demissus.*

GEOGRAPHIC DISTRIBUTION

Following are locality records deemed significant additions to previously known ranges. State names in capital letters indicate new state records. Most of the specimens listed are in the Snow Entomological Museum, University of Kansas (SEM). Specimens in parentheses not seen, identified by Wes Bicha.

Panorpa anomala Carpenter. INDIANA, Elkhart Co., 26 July 1980 (1 male, 5 females); Jackson Co., 19 May 1979 (2 males, 2 females); Jennings Co., 27 June 1987 (2 males); Kosciusko Co., 26 July 1980 (1 male), 24 July 1981 (2 males, 1 female); Starke Co., 11 July 1979 (2 males), 8 Aug. 1979 (3 males, 1 female), 8 Aug. 1980 (1 male, 1 female); all collected by Wes Bicha and in his collection. The species has been recorded earlier from Illinois, Kansas and southward.

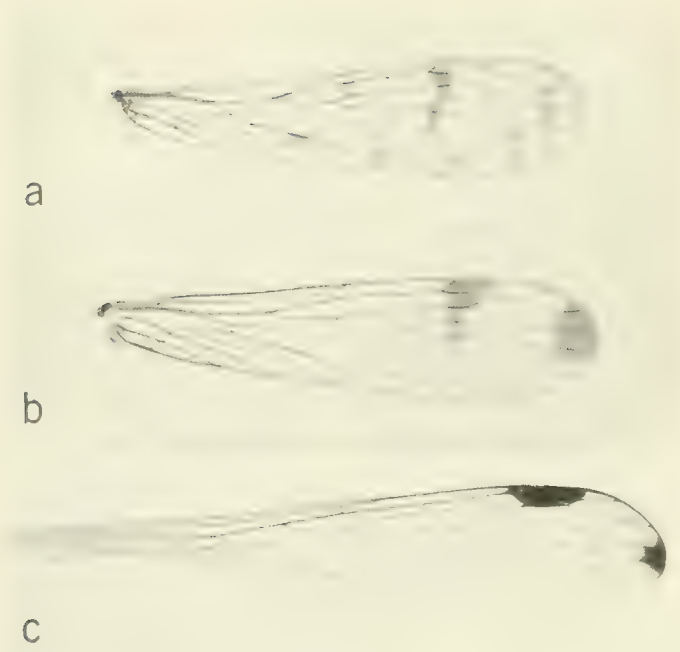


Fig. 99. Right fore wings of Mecoptera. a, *Panorpa involuta* n. sp., male paratype. b, *Panorpa bimacula* n. sp., male paratype. c, *Kalobittacus maniculatus* n. sp., female paratype (small spur veins in first cell M_1 are not typical).

Panorpa bichai Byers. INDIANA, Monroe Co., 9.6 km SE of Bloomington, 1 Sept. 1994, D. M. Windsor - 1 male (SEM); previously recorded only from Tennessee.

Panorpa consuetudinis Snodgrass. ALABAMA, Macon Co., 31 Aug. 1984, Wes Bicha (1 male, 4 females; WB); recorded earlier from as near as Mississippi.

Panorpa dubitans Carpenter. Wes Bicha adds the following counties in Indiana in which *dubitans* has been found by him: Jasper Co., 10 July-1 Aug.; St. Joseph Co., 24 July; White Co., 11-24 July. The type locality is Hessville, near Hammond, Lake Co., Indiana.

Panorpa ensigera Bicha. SOUTH CAROLINA, Marion Co., 10 Oct. 1993, Wes Bicha (4 males, 4 females; WB); Marlboro Co., 9 Oct. 1993, Wes Bicha (2 males, 4 females; WB). Species previously recorded from North Carolina.

Panorpa hungerfordi Byers. INDIANA, Brown Co., 24 August 1985 (2 males); Cass Co., 22-24 Aug. 1980 (1 male, 2 females); Jasper Co., 11 Sept. 1979 (8 males, 1 female); Marshall Co., 8 Aug. 1980 (4 males); Pulaski Co., 11 Sept. 1979 (1 male, 2 females), 23 Aug. 1980 (1 female), 21 Aug. 1981 (2 males, 2 females); Starke Co., 21-24 Aug. 1981 (19 males, 19 females); White Co., 29 Aug. 1980 (6 males); all collected by and in the collection of Wes Bicha.

Panorpa submaculosa Carpenter. INDIANA, Brown Co., 2 June 1976 (2 males), 19 May 1979 (4 males, 3 females), 21 May 1981 (14 males, 9 females); Lagrange Co., 13 June 1979 (2 males); all collected by and in the collection of Wes Bicha.

Bittacus occidentis Walker. SOUTH DAKOTA, Jackson Co., Big Buffalo Creek N of Cedar Pass, 8 July 1964, D. G. Ferguson - 1 male (USNM). This widespread species has been found from western New York southward to South Carolina and Alabama, westward to Iowa and Nebraska and southwestward to Texas and Arizona.

Bittacus panamensis Byers. Venezuela, Guarico Hato, Masaguaral, 24 km S of Calabozo, 20-28 May 1985, Menke and Carpenter - 1 male (USNM); Costa Rica, 14 km S of Cañas, 24-31 Aug. 1990, F. D. Parker - 1 male (USU); previously recorded from Panama and Trinidad.

Bittacus pilicornis Westwood. ALABAMA, Winston Co., 8.9 km NE of Double Springs, 19 May 1993, G. W. Byers - 6 males, 9 females; MISSISSIPPI, Lee Co., Tombigbee State Park, SE of Tupelo, 18 May 1993, G. W. Byers - 2 males, 6 females; Winston Co., 16 km NE of Louisville, Tombigbee National Forest, 18 May 1993, G. W. Byers - 1 male, 7 females; LOUISIANA, Winn Parish, Gum Springs Recreation Area, Kisatchie National Forest, 17 May 1993, G. W. Byers - 2 males, 4 females; TEXAS, Cherokee Co., U.S. Hwy. 69, 7.4 km N of Jacksonville, 14 May 1993, G. W. Byers - 5 males, 3 females; Houston Co., 45 km W of Lufkin, 14 May 1993, G. W. Byers - 3 males, 3 females; Jasper Co., Boykin Springs, Angelina National Forest, 24 km NW of Jasper, 16 May 1993, G. W. Byers - 1 male, 2 females; San Augustine Co., Piney Woods Conservation Center, about 17 km SE of Broaddus, at light, 15 May 1993, G. W. Byers - 1 male, 1 female; all in SEM. Wes Bicha adds the following locality-date information based on specimens in his collection: ALABAMA, Coosa Co., 28 May 1989 (1 male, 1 female); DeKalb Co., 27 May 1989 (2 males, 2 females); Lawrence Co., 31 May 1982 (1 male, 2 females); Marion Co., 30 May 1982 (1 female); Pike Co., 23 May 1986 (1 female); Winston Co., 30 May 1982 (1 female); MISSISSIPPI, Hinds, Co., 25 April 1981 (1 male); Lauderdale Co., 24 May 1986 (2 females); Lee Co., 30 May 1982 (3 females). A widespread species, *B. pilicornis* was recorded earlier from Massachusetts westward to Wisconsin, Kansas and Arkansas and southward to northern Florida; somehow it was not recorded previously from farther southwest, for it was fairly common at every likely habitat sampled, from eastern Texas to Alabama.

Bittacus punctiger Westwood. ALABAMA, Hale Co., Payne Lake, Talladega National Forest, about 38.5 km SE of Tuscaloosa, 25 May 1978, G. W. Byers - 3 males, 3 females (SEM). Since the only earlier record from Mississippi was without complete data, Wes Bicha provides the following: Lauderdale Co., 24 May 1986 (1 female). This species was already known from Maryland westward to Indiana and Texas, southward to Florida, so these records are not surprising.

Bittacus strigosus Hagen. ALABAMA, Limestone Co., 30 May 1982, Wes Bicha (4 males; WB); Marion Co., 30 May 1982, Wes Bicha (1 male, 1 female; WB). WYOMING, Converse Co., 16 km S of Douglas, 27 Aug. 1962, W. J. Hanson - 1 male, 1 female (SEM). The species had previously been recorded from New England and New York westward to Manitoba and Montana and southward to Arkansas and South Carolina.

Hylobittacus apicalis (Hagen). ALABAMA, Lawrence Co., 31 May 1982, Wes Bicha; (1 female; WB); Limestone Co., 30 May 1982, Wes Bicha (2 females; WB).

LITERATURE CITED

Banks, N. 1913. Synopses and descriptions of exotic Neuroptera. Transactions of the American Entomological Society 39:201-242, plates 23-26.

Byers, G. W. 1958. Descriptions and distributional records of American Mecoptera. Journal of the Kansas Entomological Society 31:213-222.

_____ 1962. Descriptions and distributional records of American Mecoptera. II. Journal of the Kansas Entomological Society 35:299-307.

_____ 1965. New and uncommon neotropical Mecoptera. Journal of the Kansas Entomological Society 38:135-144.

_____ 1993. Autumnal Mecoptera of southeastern United States. University of Kansas Science Bulletin 55:57-96.

_____ 1994. Mexican species of *Kalobittacus* Esben-Petersen (Mecoptera: Bittacidae). The Canadian Entomologist 126:1093-1099.

Carpenter, F. M. 1931. Revision of the nearctic Mecoptera. Bulletin of the Museum of Comparative Zoology at Harvard College 72:205-277, plates 1-8.

Esben-Petersen, P. 1921. Mecoptera. Collections Zoologiques du Baron Edm. de Selys Longchamps, Fasc. 5. Hayez, Bruxelles, 172 pp., 2 plates.

Issiki, S. 1929. Descriptions of new species of the genus *Panorpa* from Japan and Formosa. Journal of the Society of Tropical Agriculture 1:182-191.

Klug, J. C. F. 1838 (1836). Versuch einer systematischen Feststellung der Insecten-Familie: Panorpatae und Auseinandersetzung ihren Gattungen und Arten. Abhandlungen, Akademie der Wissenschaften in Berlin, pp. 81-108, plate I.

Navás, L. 1932. Alcuni insetti del Museo di Zoologia della R. Università di Torino. Bolletino dei Musei di Zoologia e di Anatomia Comparata della R. Università di Torino, vol. 42 (ser. 3) no. 26:1-38.

Papavero, N. 1971. Essays on the history of neotropical dipterology. Vol. I., 216 pp. Museu de Zoologia, Universidade de São Paulo. ("Ferdinand Deppe's travels in Mexico" appears on pp. 103-107.)

Penny, N. D. and J. R. Arias. 1982. Notes on Amazonian Bittacidae (Mecoptera) with the descriptions of two new species. Memorias do Instituto Oswaldo Cruz, Rio de Janeiro, 77:263-274.

ANNOUNCEMENT

The *University of Kansas Science Bulletin* (continuation of the *Kansas University Quarterly*) is an outlet for scholarly scientific investigations carried out at the University of Kansas or by University faculty and students. Since its inception, volumes of the *Bulletin* have been variously issued as single bound volumes, as two or three multi-paper parts or as series of individual papers. Issuance is at irregular intervals, with each volume prior to volume 50 approximately 1000 pages in length. Effective with volume 50, page size has been enlarged, reducing the length of each volume to about 750 pages.

The supply of all volumes of the *Kansas University Quarterly* is now exhausted. However, most volumes of the *University of Kansas Science Bulletin* are still available and are offered, in exchange for similar publications, to learned societies, colleges and universities and other institutions, or may be purchased at $30.00 per volume. Where some of these volumes were issued in parts, individual parts are priced at the rate of 3 cents per page. Current policy, initiated with volume 46, is to issue individual papers as published. Such separata may be purchased individually at the rate of 7 cents per page, with a minimum charge of $1.50 per separate. Subscriptions for forthcoming volumes may be entered at the rate of $30.00 per volume. All communications regarding exchanges, sales and subscriptions should be addressed to the EXCHANGE LIBRARIAN, UNIVERSITY OF KANSAS LIBRARIES, LAWRENCE, KANSAS 66045.

Reprints of individual papers for personal use by investigators are available for most recent and many older issues of the *Bulletin*. Such requests should be directed to the author.

The International Standard Serial Number of this publication is US ISSN 0022-8850.

Editor
Charles D. Michener

Editorial Board
Meredith Lane, *Chairman*
James S. Ashe
George W. Byers
Christopher Haufler
Norman A. Slade

THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. 55, No. 15, pp. 549-634 July 5, 1996

Phylogeny and Revision of the Genera of Cryptophagidae (Coleoptera: Cucujoidea)[1]

RICHARD A. B. LESCHEN [2,3]

TABLE OF CONTENTS

Introduction 550
Classification of Cryptophagidae, 551; Natural History, 551; Notes on Adult Morphology, 554
Materials and Methods 554
Phylogenetic Analysis 555
Monophyly and Relationships of Cryptophagidae, 555; Terminal Taxa, 556; Cladistic Methods, 557; Character Analysis, 557; Results, 571
Major Lineages and Taxonomic Conclusions 571
Cryptophagini ,573; Cryptosomatulini, 575; Caenoscelini, 575; Hypocoprini, 576; Atomariini, 576; Cryptafricini, 577
Problematic Characters and Their Impact on Phylogenetic Structure 577
Diet and Inquilinism, 577; Hind Wing Reduction or Loss, 579; Hind Wing Vein Losses, 580
Family Cryptophagidae 581
Key to the Genera and Higher Taxa of Cryptophagidae 583
Cryptophaginae. 586
Cryptophagini 587
Antherophagus Dejean, 587; *Asternodea* n. gen., 589; *Catopochrotus* Reitter, 589; *Cryptophagus* Herbst , 590; *Henoticus* Thomson, 592; *Henotiderus* Reitter, 594; *Henotimorphus* Ljubarsky, 595; *Micrambe* Thomson, 596; *Mnionomidius* Reitter, 596; *Mnioticus* Coombs and Woodroffe, 597; *Myrmedophila* Bousquet, 597; *Neohenoticus* n. gen., 598; *Paramecosoma* Curtis, 599; *Pteryngium* Reitter, 599; *Salebius* Casey, 600; *Serratomaria* Nakane and Hisamatsu, 600; *Spaniophaenus* Reitter, 601; *Spavius* Motschulsky, 602; *Striatocryptus* n. gen., 602; *Telmatophilus* Heer, 603
Cryptosomatulini. 605
Neopicrotus n. gen., 606
Caenoscelini 607
Caenoscelis Thomson, 607; *Dernostea* Sasaji, 608; *Himascelis* Sen Gupta, 608; *Sternodea* Reitter, 608
Atomariinae 608
Hypocoprini 610
Alfieriella Wittmer, 610; *Amydropa* Reitter, 610; *Hypocoprus* Motschulsky, 612; *Hypophagus* Ljubarsky, 612
Atomariini 614
Atomaria Stephens, 614; *Atomaroides* Ljubarsky, 615; *Chilatomaria* n. gen., 616; *Curelius* Casey, 617; *Ephistemus* Stephens, 619; *Microatomaria* n. gen., 619; *Ootypus* Ganglbauer, 621; *Paratomaria* n. gen., 621; *Salltius* Broun, 623; *Tisactia* Casey, 623
Cryptafricini 623
Cryptafricus n. gen., 624; *Cryptogasterus* n. gen., 624; *Anitamaria* n. gen., 625; *Microphagus* n. gen., 626
Acknowledgments 626
Literature Cited 627
Appendix. Taxa of Cryptophagidae and related Cucujoidea examined 632

[1] CONTRIBUTION NUMBER 3178 FROM THE DEPARTMENT OF ENTOMOLOGY, UNIVERSITY OF KANSAS, LAWRENCE, KANSAS 66045, U.S.A.
[2] SNOW ENTOMOLOGICAL MUSEUM, UNIVERSITY OF KANSAS, LAWRENCE, KANSAS, 66045, U.S.A.
[3] PRESENT ADDRESS, DEPARTMENT OF ENTOMOLOGY, MICHIGAN STATE UNIVERSITY, EAST LANSING, MICHIGAN, 48824, U.S.A.

ABSTRACT

A revision of the higher level classification of the cucujoid family Cryptophagidae is provided. The revision is based on a cladistic analysis of 55 genus-level terminal taxa representing most of the described higher taxa. At least 500 trees were produced in an analysis without character weighting, nine were produced using successive approximations weighting. Revision of the classification was based on all trees produced and the proposed classification includes groups that were shown to be monophyletic in the cladistic analysis. There are two recognized subfamilies; Cryptophaginae Kirby, with three tribes and 30 genera, and Atomariinae Stephens (Alfieriellinae Crowson and Hypocoprinae Reitter are junior synonyms), with three tribes and 18 genera. The cryptophagine tribe Cryptophagini Kirby contains 20 genera, three of which are described as new. These are *Asternodea* (type species *Asternodea loebli* new species), *Neohenoticus* (type species *Neohenoticus palmerae* new species), and *Striatocryptus* (type species *Striatocryptus wilkinsoni* new species, also *S. polyglandis* new species). The cryptophagine genera *Cryptophagus* Herbst and *Micrambe* Thomson are shown to be separate and unrelated taxa, and many species previously included in *Cryptophagus* are transferred to *Micrambe* resulting in 40 new combinations. *Henotiderus hirtus* Casey is a synonym of *Henotiderus obesulum* Casey while *Pteryngium duclouxi* Grouvelle is transferred to *Micrambe*. The cryptophagine tribe Caenoscelini Casey contains four genera. The cryptophagine tribe Cryptosomatulini Crowson (the tribe Picrotini Crowson is a junior synonym) contains 10 genera, one of which is described as new: *Neopicrotus* (type species *Neopicrotus peckorum* new species). The two species *Picrotus pensus* Broun and *Picrotus sanguineus* Broun are synonyms of *Picrotus thoracicus* Sharp. The atomariine tribe Atomariini LeConte (the tribes Salltiini Crowson and Ephistemini Casey are junior synonyms) contains 10 genera, three of which are described as new. These are: *Chilatomaria* (type species *Chilatomaria hillersae* new species), and includes *Chilatomaria lindensis* (Blackburn) new combination and *Chilatomaria australis* (Blackburn) new combination; *Microatomaria* new genus (type species *Microatomaria hintoni* new species); and *Paratomaria* (type species *Paratomaria crowsoni* new species). A new tribe of Atomariinae is described for four new genera. It is: Cryptafricini (type genus: *Cryptafricus*); *Cryptafricus* (type species *Cryptafricus leleupi* new species); *Cryptogasterus* (type species *Cryptogasterus lawrencei* new species); *Anitamaria* (type species *Anitamaria thayerorum* new species); and *Microphagus* (type species *Microphagus johnsoni* new species). The tribe Hypocoprini contains three genera. The type species of *Amydropa* Reitter (*Amydropa anophthalma* Reitter) is redescribed and a new species (*Amydropa clarki*) is added to the genus. Problematic characters, hind wing loss and reduction, hind wing venation, and behaviors, and how they relate to character coding and character evolution are discussed. Natural history information is reviewed for the family.

INTRODUCTION

Over 10 years ago, Lawrence and Newton (1982) reviewed the systematics of Cucujoidea. Three major advancements they recognized included the erection of several south temperate families, the recognition of the Cerylonid series as a distinct monophyletic group, and the transfer of taxa from the "old" Cryptophagidae primarily into Languriidae. These advances were made by R. A. Crowson and T. Sen Gupta in several studies on cucujoid beetles (1955, 1967, 1968a, 1968b, 1969a, 1969b, 1971). The removal of taxa from the Cryptophagidae by Crowson and Sen Gupta, therefore, set the stage for further work on the systematics of the probably monophyletic Cryptophagidae. The major goals of the present study are to examine the phylogenetic relationships of Cryptophagidae using cladistic analysis, revise the classification of higher taxa in the family, and review the currently recognized genera. The south temperate tribe Cryptosomatulini is treated superficially because of the large number of undescribed species and uncertain taxonomic status of the described species.

The family Cryptophagidae is a moderately large group of small-sized beetles (length 1-6 mm) containing over 600 described species placed in about 50 genera and in six subfamilies (Appendix). Only a few genera have received species-level revisions and these were on a local basis (e.g., Coombs and Woodroffe 1955, Johnson 1992, Woodroffe and Coombs 1961, Bousquet 1989, Ljubarsky 1987a, 1992b). The monophyly of the higher taxa has not been established by rigorous cladistic analysis and the taxonomic definition of many genera is unclear. Most of the described species diversity is contained within the genera *Atomaria* (186 species), *Cryptophagus* (198 species), and *Micrambe* (89 species), and many taxonomic problems are present among these. Many of the other genera have not been treated since their original descriptions.

Cryptophagidae has a world-wide distribution, and as indicated by Crowson (1980), some groups have amphipolar distributions, i.e., pairs of sister taxa are distributed separately in regions north and south of the equator. The cryptophagine tribes Cryptosomatulini and Picrotini (both Cryptophaginae) are found in south temperate regions, while Caenoscelini are mainly Holarctic and somewhat circumtropical. Cryptophagini are largely Holarctic with only a few species that occur in equatorial regions; however, many species of *Micrambe* and all *Mnioticus* occur in Africa while a species representing an undescribed genus in this tribe occurs in Chile. Members of Atomariinae are found world-wide with most species in the Holarctic region. An undescribed group of species similar in form to Atomariini is circumtropical, as are most members of Ephistemini. Hypocoprinae are Holarctic while Alfieriellinae are predominately Mediterranean and are associated with drier habitats.

The fossil history of Cryptophagidae is poorly known. Several contemporary genera, *Antherophagus*, *Atomaria*, *Cryptophagus*, *Spavius*, *Micrambe*, and *Telmatophilus*, are listed

MCZ LIBRARY

from Oligocene Baltic amber by Spahr (1981), while the extinct Cretaceous genera *Nganasania* Zherichnin 1977 and *Cryptophagites* Ponomorenko 1990 are doubtfully placed in the family. I have not examined these specimens and their exact identities require confirmation.

Another feature of Cryptophagidae is the large number of undescribed species- and genus-level taxa. This is true for groups of microcoleoptera that have not attracted many specialists. As a result, many presently recognized genera of Cryptophagidae are poorly defined and many species described from south temperate regions are incorrectly placed in Holarctic genera (most of these species belong in separate genera), although a few are Holarctic species dispersed to these regions via human trade.

Cryptophagidae is one of 31 families in Cucujoidea; the relationships among these families are largely unknown. Crowson (1955, 1960) recognized at least one (possibly) monophyletic group among Cucujoidea, the Cerylonid series; and, this group has received recent attention by several workers (Pal and Lawrence 1986, Ślipiński 1990, Ślipiński and Pakaluk 1991). The remaining groups constitute what cucujoid workers call the "lower Cucujoidea." Among the lower cucujoids are several probably monophyletic groups: Sphindidae + Protocucujidae (Thomas 1984a, Burakowski and Ślipiński 1987, McHugh 1992); Laemophloeidae (including Propalticidae) + Phalacridae + Passandridae (Thomas 1984b); Erotylidae + Languriidae (Sen Gupta 1969, Leschen unpublished); Nitidulidae + Cybocephalidae + Kateretidae + Smicripidae (Audisio 1994; also recognized as Nitiduloidea by Crowson, unpublished). The monophyly of these has not been rigorously demonstrated while the remaining members of the lower Cucujoidea (i.e., Monotomidae, Boganiidae, *Cyclaxyra* [Phalacridae], Helotidae, Lamingtoniidae, Passandridae, Phloeostichidae) have uncertain affinities. The group I refer to as the "cucujid line" in this paper includes the following families: Cucujidae, Hobartiidae, Phloeostichidae (actually composed of several lineages; Crowson and Ślipiński, unpublished), Cryptophagidae, Cavognathidae, and Silvanidae (see also Thomas 1984a). This informal grouping of families constitutes the quintessential cucujoid — most members are small-sized, brown and setose, and generally elongate and somewhat flattened. The enigmatic positions of numerous taxa and ambiguous relationships among members of Cucujoidea make this superfamily particularly challenging for higher level systematic studies.

Classification of Cryptophagidae: Because changes will be made in the classification of Cryptophagidae as a result of the studies described herein, a brief historical review of the higher taxonomic categories is necessary. For the history of genera, type species, and notes on synonymy of family-group names, see the sections on Taxonomic Treatment and Pakaluk et al. (1995). Taxonomic ranks of family-group names as follows are confusing and reflect that indicated in the original publications.

Kirby (1837) proposed the family name Cryptophagidae for the genus *Cryptophagus*, which included one species originally described as *Dermestes cellaris* Scopoli and two species of *Atomaria*. LeConte (1861) recognized three tribes in his revision of Cryptophagidae: Atomariini, Cryptophagini, and Telmatophilini (first established as Telmatophilides by Jacquelin du Val [1859]). The Telmatophilini were also treated as a separate family by Reitter (1879, 1885) but are presently included in the subfamily Cryptophaginae (Reitter 1887; Crowson 1980). LeConte (1861) recognized two groups within Cryptophagini: Antherophagi and Cryptophagi. Subsequently, Reitter (1875) added Paramecosomina while Casey (1900) added Spaniophaeni and Emphyli (originally proposed for the genus *Emphylus* Erichson but see Bousquet 1989) to the Cryptophaginae. Casey (1900) also established Caenoscelini (for *Caenoscelis*) and Sternodeini (for *Sternodea*), originally placed among Atomariinae by Reitter (1875), but these were later transferred to Cryptophaginae and are included as a single tribe by Crowson (1980). Recently, Crowson (1980) added the tribes Cryptosomatulini and Picrotini to Cryptophaginae.

The Atomariinae (treated as a family by Crotch 1873) is currently composed of the tribes Atomariini LeConte (1861), Ephistemini Casey (1900), and Saltiini Crowson (1980).

Hypocoprinae Reitter (1879) has been considered either as a separate family (Crowson 1955) or included by several authors as a tribe in Cucujidae (Reitter 1879, Hetschko 1930) or other families, and is presently placed in Cryptophagidae (Crowson 1980).

Catopochrotidae was established for the myrmecophilic genus *Catopochrotus* described by Reitter (1889) and was later included in Cryptophagidae by Lawrence (1982).

Crowson (1980) erected the subfamily Alfieriellinae for the enigmatic genus *Alfieriella* Wittmer (= *Cyprogenia* Baudi) that was first included in Cucujidae but is presently placed in Cryptophagidae. Ratti (1976) considered *Alfieriella* closely related to *Hypocoprus* which was placed in the cucujid tribe Hypocoprini by Reitter (1879) and Hetschko (1930). Subsequently, the tribe Hypocoprini was included in Cryptophagidae by Reitter (1911) while *Hypocoprus* was included in Monotomidae by Leng (1920). Crowson (1955) treated *Hypocoprus* as a member of the monogeneric family Hypocoprinae, and later (Crowson 1967) suggested that *Hypocoprus* may be a cryptophagid. Presently Crowson (1980) considers *Hypocoprus* a member of Hypocoprinae, a monogeneric subfamily of Cryptophagidae.

As mentioned earlier, a variety of genera originally included as members of the cryptophagid tribes Cryptophagini, Telmatophilini, Loberini, and Cryptophilini (see Schenkling 1923), are presently placed in Languriidae (see papers by Crowson and Sen Gupta). Other genera removed from Cryptophagidae are placed in other families (Biphyllidae, Cavognathidae, Chrysomelidae, Cleridae, Erotylidae, Phalacridae, and Salpingidae [= Elacatidae]). These transfers of genera to other families are listed in Bousquet (1989) and Johnson and Leschen (in preparation).

Natural History: Most detailed information on the natural histories of cryptophagids is based on studies of economi-

cally important species that are stored product pests or attack a few garden plants (Hinton 1945, Newton 1932). Most members of Cryptophagidae occur in leaf litter, compost piles, animal nests, and rotting wood where they feed on spores, hyphae, and conidia of microfungi; a few species, however, are reported from macrofungi (Falcoz 1929, Donisthorpe 1935, Hinton 1945, Benick 1952, Lawrence 1991, Cooter 1991). Examination of gut contents reveals a variety of spore types (e.g., conidiospores, phragmaspores, simple spores, etc.) indicating that there may be different patterns of host association with microfungi. A case of polyphagy, for example, is given by Hinton (1945) who was able to maintain cultures of the stored product pest *Cryptophagus acutangulus* Gyllenhal on 12 species of microfungi including Basidiomycetes, Ascomycetes, Zygomycetes, and imperfect fungi. Other polyphagous *Cryptophagus* species are incidental pests of stored products (Falcoz 1929, Hinton 1945). Monophagy is suggested for the North American species *Henotiderus obesulus* (Casey) which has been collected on a few polypore fungi (Weiss and West 1920). I have collected and reared larvae and adults exclusively from *Cladobotrium* sp., a fungus parasitic on polypores (this species may be the imperfect stage of *Hyphomyces*, an ascomycete parasitic on fleshy Basidiomycetes; B. Horn, personal communication) from different locations in eastern North America (Ontario, Arkansas).

There may be mutual benefits between cryptophagid predators and the microfungi on which they feed, as indicated for other beetle-fungus interactions (Blackwell 1984, Crowson 1984). Conidia of *Penicillum* fed on by adults of *C. acutangulus* showed a 15% survival rate after passing through the gut and had a faster germination rate than unprocessed conidia (Hinton and Stephens 1941). Spores and conidia carried in the gut and passively on the exterior parts of the body of beetles may disperse to new habitats. Although spore filled mycangia (invaginated cuticular structures on the body that contain fungal spores) are present on the bodies of Latridiidae, Silvanidae, and Sphindidae, which also feed on microfungi, I have not observed large numbers of spores inside mycangium-like structures in specimens of Cryptophagidae.

Specific fungal host patterns have been observed for species that feed on the tissues of large Basidiomycetes. Adults and larvae of *Pteryngium crenatum* (Fabricius) are often collected from *Fomitopsis* and *Trichaptum* spp. (Basidiomycetes) fruiting bodies in Europe and in the western part of its range in North America (Falcoz 1929, Scheerpeltz and Höfler 1948, Horion 1960, Koch 1989, J. F. Lawrence, personal communication). Two species of cryptophagids have been consistently collected from Gasteromycetes and other puffball-like fungi: adults and larvae of an undescribed species from eastern Australia (*Cryptogasterus*) and adults of *Cryptophagus lycoperdi* (Scopoli) (Falcoz 1929, Donisthorpe 1935, Scheerpeltz and Höfler 1948, Benick 1952). Specimens of *Cryptophagus maximus* Blake and *C. enormis* Hisamatsu, possibly related species from California and Japan respectively, occur inside the pouch fungus *Cryptoporus volvatus* (Blake 1928, Hisamatsu 1962, Lawrence 1991, Setsuda 1995). Adults of *Atomaria fimetarii* (Fabricius) have been collected from *Coprinus comatus* in Europe and North America (Donisthorpe 1935, Cooter 1991, Johnson 1993, personal observation) while those of *A. umbrina* (Gyllenhal) occur on *Pholiota* and *Armillaria* (Johnson 1993).

Cryptophagids rarely occur on Ascomycetes with large fruiting bodies; adults of *Cryptophagus ruficornis* Stephens and *C. dentatus* (Herbst) have been collected from the fruiting bodies of *Daldinia* (Donisthorpe 1935, Palm 1951, Hingley 1971, Lawrence 1991, Cooter 1991).

Some cryptophagids also feed on spores and pollen produced by vascular plants. Adults of the Chilean genus *Cryptothelypterus* have been collected from ferns, and an analysis of gut contents showed that their diet consists almost entirely of fern spores (Leschen and Lawrence 1991). Adults of some species of *Micrambe* and *Mnioticus* have been collected from the flowers of high altitude *Lobelia*, *Senecio*, and *Helichrysum* in East Africa (Scott 1935). However, label data on hundreds of specimens in the collection of the Natural History Museum, London, and information from gut contents, suggest that these African beetles are found in a variety of decaying habitats and leaf litter and may not be exclusive to flowers. Adult specimens of some European members of *Micrambe* are commonly collected from flowers (Falcoz 1929; personal observation), as are some species of south temperate Atomariinae (described herein) that occur on plants and have guts filled with pollen. All species of *Telmatophilus* are associated with aquatic plants of the genera *Carex*, *Sparganium*, and *Typha* (Falcoz 1929, Horion 1960, Hatch 1962, Lawrence 1991). Adults can be collected from the plants' sheaths (Cooter 1991), and on the flower heads where they feed on pollen, mate, and oviposit; larval development occurs in male flowers. Host patterns are so well defined for these species that adults of *Telmatophilus typhae* Fallén and *T. caricis* Olivier that were present at a single pond in England were restricted to their obligate hosts *Typha latifolia* and *Sparganium erectum* respectively (personal observation). Adult specimens of *Antherophagus* have been collected at flowers, but it is not clear if these were waiting for foraging *Bombus* bees (see below) or were feeding on pollen and nectar; adults and larvae extracted from *Bombus* nests have guts filled with pollen and presumably feed on bees' provisions, fecal material, and other debris in the nest. Occasional specimens of adults of *Caenoscelis*, *Atomaria* and *Cryptophagus* are collected from flowers, but these are probably incidental host records, and it is likely that none of these genera contains species that are pollen specialists.

Most cryptophagids appear to be limited to diets of similar physical shape and size: spores, hyphae, and pollen. The restriction of diet to small, loosely organized particles appears to be associated with a particular type of mouthpart structure adapted for microphagy (Lawrence 1988, Leschen and Lawrence 1991, Leschen 1993). However, feeding on more compact foods occurs in some species of *Atomaria*. Newton (1932) reported on the phytophagous habits of *Atomaria linearis* Stephens, a pest of marigolds and other plants. Apparently significant damage to germinating seeds can be caused by adults, but after the cotyledon stage, survival of

host plants is high. Larvae were reared on the root systems of plants; however, complete development to adults was not mentioned. Many species of *Atomaria* are found in habitats associated with grass and decaying vegetable matter (Johnson 1993), and it is possible that diets of these species include other types of food besides fungi. Recent collections of an undetermined species of *Chiliotis* (Cryptosomatulini) made by me in southern Chile indicate another compact food source used by cryptophagids. Numerous larvae and adults were observed to feed on strange gall-like growths on vines that entangled *Nothophagus* trees. These growths appear to be plant material and contain no evidence of fungal tissue (R. Lichtwardt, personal communication).

Some species of Cryptophagidae occur in unusual habitats. For example, some adult specimens of European *Micrambe* are found in nests of gregarious caterpillars (Falcoz 1929) as well as decaying flowers (*Micrambe vini* [Panzer]). Also, adults of *Cryptophagus* and a few *Atomaria* are collected frequently from mammal and bird nests (Falcoz 1929, Hicks 1959, 1962, 1971, Woodroffe and Coombs 1961, Cooter 1991, Johnson 1993, Karl Stephan, personal communication, Paul Skelley, personal communication). *Paramecosoma melanocephalum* Herbst occurs in flood debris at the edges of rivers and streams in Europe (Falcoz 1929). Many adult specimens collected in England were in fist-sized clumps of flood debris that accumulated at the tips of branches hanging over the river while larvae were more common in larger accumulations at the river bank (C. Johnson and R. Leschen, personal observation). Members of *Ootypus globosus* (Waltl) and certain species of *Atomaria* are commonly collected in horse manure at a specific stage of decay and moisture content (Cooter 1991, Johnson 1993).

A few species of cryptophagids occur as inquilines in the nests of termites, ants, bees, or wasps. Members of the genus *Hypocoprus* have been collected in ant nests of the genus *Formica*, leaf litter, and large mammal dung (Motschulsky 1844, Crowson 1955; J. L. Carr, personal communication; C. Johnson, personal communication), but the species may not be true inquilines. Some European species of *Cryptophagus* have been collected from nests of *Bombus* and other ground-nesting bees, ground-nesting and tree-nesting wasps (*Vespa* and *Dolichovespula*), and ants (Falcoz 1929, Hinton 1941, Coombs and Woodroffe 1955, Cooter 1991); however, despite their occurrence in other habitats, these species are probably obligate rather than facultative inquilines. Species of *Spaniophaenus* have been collected as adults from termite (*Acanthotermes ahngerianus* [Jacobson]) and ant (*Aphaenogaster barbara* [Chobaut]) nests (Falcoz 1929, Kieseritzky and Reichardt 1936). *Spavius* and *Myrmedophila* occur in *Formica* nests (Motschulsky 1844, Schwarz and Ulke 1891, Eichelbaum 1907, Horion 1960, Bousquet 1989) in Europe and North America respectively; both are reddish-brown in color and have reduced vestiture over the body. The last three genera all appear very similar to *Cryptophagus* in body form (compare Figs. 180, 186, 190), although members of *Spaniophaenus* and *Spavius* have the head slightly retracted into the prothorax. The extraordinary species *Catopochrotus crematogastri* Reitter is an obligate inquiline that occurs with ants of the genus *Crematogaster* (Reitter 1889, Kistner 1982). Members of this species are highly modified and have a "limuloid" body form (Figs. 178, 179), clavate antennae (Fig. 33), the head withdrawn almost entirely into the prothorax, and flattened legs. The variation in adult body forms among the above species may indicate different levels of behavioral integration into nests of their social insect hosts.

Members of the genus *Antherophagus* are well-known for their occurrence in nests of *Bombus* bees; I will not review all the literature here (see Chavarria 1994a, 1994b, Leschen, in preparation). The species of this genus are robust (Fig. 174), among the largest of Cryptophagidae, and adults are usually golden-brown in color. *Antherophagus* is broadly sympatric with *Bombus*, although the distribution of the bees is broader than that of the beetles. For example, North American species of *Bombus* are present throughout the continent but *Antherophagus* is limited to northern and montane regions in the east and west. Some species of *Antherophagus* are reported to be phoretic as adults on *Bombus*, and are found attached to the legs and mouthparts of the bees (Wheeler 1919, Donisthorpe 1920, Meer Mohr and Lieftinck 1947, Chavarria 1994a). This phenomenon is documented for species occurring in the Holarctic, Nearctic and southeast Asia, and there are several unpublished records for species occurring in Venezuela and Brazil (R. Brooks, C. Marshall, D. Roubik, F. Silveira, personal communications). Presumably, adults of flight-capable species wait for bees at flowers, attach to foraging bees, and are carried into the nests where oviposition and larval development ensue. Although some members of *Antherophagus* are reported to be phoretic, in some populations in Alberta, Canada, adults were present in considerable numbers in the nests suggesting that some individuals may fly directly to nests (K. Richards, personal communication).

Some groups of *Bombus* that occur in tropical regions also serve as hosts to species of *Antherophagus*, and some of these beetles are flightless and have a reduced number of eye facets (e.g., *Antherophagus ruficornis* Grouvelle in Brazil and *Antherophagus ludekingi* Grouvelle from Java and Sumatra). The only way in which these flightless beetles can disperse to new *Bombus* nests is by phoresy. This suggests that there is a grade of behaviors from nonphoretic (those populations in Canada) to phoretic populations among species of *Antherophagus*. While larval phoresy is common in Rhipiphoridae and Meloidae (Crowson 1981), phoresy by adult beetles is rare, reported for some scotocryptine Leiodidae (Roubik and Wheeler 1982) and *Antherophagus*. Also, male specimens of *Antherophagus* have a prominent notch on their clypeus (Figs. 34, 175): Is this feature associated with phoresy and are both sexes phoretic? A thorough study of the behavior and phylogeny of *Antherophagus* would provide exciting new insights into the evolution of phoresy.

Several species of *Cryptophagus*, a few *Atomaria*, and *Henoticus californicus* (Mannerheim) are pests in stored products (Hinton 1945, Delobel and Tran 1993). Typically, these species are incidental pests in grains, dried fruits, and spices, and occur in situations where fungi are already present in

the stored products.

Mating and other behaviors have rarely been observed (*Atomaria:* Newton 1932, Evans 1961; *Cryptophagus*: Hinton and Stephens 1941, Hinton 1945). Females are mounted dorsally by males, and there are no records of back to back mating. Eggs are deposited singly on the fungal substrate by members of *Cryptophagus* (Hinton 1945) and there appears to be no parental care associated with egg and larval development. Cryptophagid larvae have three instars, as do larvae of some other members of the lower Cucujoidea (Hinton 1945, Leschen and Carlton 1993).

Notes on Adult Morphology: The internal soft anatomy (tracheae, alimentary canal, reproductive system, and myology) of the adult of *Atomaria testacea* Stephens was studied in detail by Evans (1961b, 1961c, 1964) as *A. ruficornis* (Marsham). The descriptive and functional work by Evans sets a standard by which future studies of internal anatomy of adult cucujoids should be judged.

Sclerotized glandular ducts (character numbers 28, 49, 50, 51, 52, 56, 61, 70, 71, 79, 80, 81 in the Character Analysis) and glandular pores (character numbers 53, 54) are widespread and variable among members of Cryptophagidae. Some of these (53 and 54) may be present only in males. Descriptions and surveys of these features will be provided in a separate paper. Other internal features, for example the metendosternite, are discussed in the Character Analysis.

Many species of Coleoptera are brachypterous or apterous (Thayer 1992), collectively referred to as hind wing reduction or loss (HWL). HWL is often exhibited by species found on islands and mountains (Roff 1990) and in Cryptophagidae occurs among taxa at the population, species, and genus levels. At the population (polymorphic) and species (monomorphic) levels, HWL has been reported among members of *Atomaria* and *Cryptophagus* (Bruce 1936, Woodroffe and Coombs 1961, Coombs and Woodroffe 1962, Johnson 1970). Also there are some species of *Caenoscelis*, *Henoticus*, and *Spaniophaenus* that exhibit HWL (C. Johnson, personal communication; personal observation). Occurrence of HWL among these species is not limited to island or montane populations and has, for example, been observed in some continental species of *Cryptophagus* and *Atomaria* (Woodroffe and Coombs 1961, Coombs and Woodroffe 1962, Colin Johnson, personal communication). Also, there are a variety of brachypterous species of *Atomaria* that occur in marshy habitats (Cooter 1991). HWL also occurs among all species of *Cryptothelypterus*, *Sternodea*, *Dernostea*, *Himascelis*, *Mninomidius*, *Mnioticus*, *Salltius*, *Picrotus*, and *Thortus* (Leschen and Lawrence 1991; Crowson 1980; personal observation), suggesting that HWL among these genera may be due, in part, to inheritance from common ancestors.

HWL is often associated with external changes (i.e., a reduction in the length of the metasternum and an overall elliptical body shape) and internal changes (modifications of the metendosternite) associated with a reduction of indirect flight muscles. These features are variable in members of *Cryptophagus* and have led to confusion about generic/subgeneric limits in this genus and its relatives (Coombs and Woodroffe 1962): this topic will be addressed later.

The pronotal margins of some members of Cryptophagidae (especially Cryptophagini) bear angularities at the anterior angles and teeth at the sides (Figs. 40, 42, 47, 50-54). Ljubarsky (1992a) examined the variation in these pronotal structures, especially those present among species of *Cryptophagus*. He suggested that the pronotal features, termed "bulldozer" structures, push the substrate in which the beetles crawl away from their bodies to accommodate the wider portions of the body along the flanks or humeri of the elytra. This is an interesting hypothesis; however, Ljubarsky was unaware that many of these features on the pronotum are associated with openings of glandular ducts, suggesting that these may serve different functions than he believed.

There are several external secondary sexual characteristics of males of cryptophagids. Most males have expanded or dilated tarsomeres (Fig. 157), usually the pro- and mesotarsomeres, that have modified spatulate setae on the undersides. In some taxa, such as some males of *Striatocryptus*, the tarsomeres are not expanded but have the modified setae. The males of most species of *Telmatophilus* have the metatibia curved and slightly elbowed (Fig. 124), especially in larger specimens (see Taxonomic Treatment). Males of *Antherophagus* have a clypeal notch as well as compact antennomeres (Fig. 34, 175). Ventrite 5 of males of *Myrmedophila* have a weak depression (Bousquet 1989) while males of some species of *Telmatophilus* have either a deep groove or depression. Other secondary sexual characteristics are mentioned in the taxonomic section (e.g., body size in *Atomaria*, setose patches on the metasterna of *Microphagus*, glandular pores and ducts in Cryptophagini).

MATERIALS AND METHODS

Dissections of adult specimens are necessary for observing many internal and microscopic characters useful for cladistic analysis and identification; morphological characters were taken from both pinned and dissected specimens. Specimens chosen for dissection were removed from their pins and cleared in cold KOH until soft internal tissues were digested. Additional bleaching in H_2O_2 was necessary for specimens with relatively dark cuticle. Specimens were then washed in water and stored in 90% alcohol until dissections were performed. Cleared specimens were dissected and either stored in glycerin or mounted semipermanently on slides in Euparal (Chroma-Gessellschaft). Euparal is an alcohol-based mounting medium that produces excellent results for transmitted light. However, specimens that could not be slide-mounted were stored and examined in glycerin. Specimens to be slide-mounted were disarticulated with minuten pins in drops of Euparal on the microslide and the parts arranged appropriately. Once the parts were stationary in their positions and did not float in the mounting medium, slide props were placed into the Euparal and the dissections placed on a slide warmer overnight. Next, additional Euparal was placed over the specimens and the cover-slip applied. Microslides were left on a slide warmer for 2-3 weeks and, after thorough drying, were stored in upright microslide boxes. Specimens prepared in the above manner could also be used for examination of gut contents.

Prepared specimens were examined with an Olympus BH2 compound microscope equipped with Nomarski differential interference contrast (DIC). Nomarski DIC was used because of the excellent resolution it offers for microstructure. Drawings were made with a drawing tube or camera lucida.

For scanning electron microscopy (SEM), specimens removed from their pins were sonicated in alcohol to remove debris, then cleaned in acetone, air-dried, and mounted on SEM stubs. The specimens were gold coated in a Hammer 2 sputter coater and examined with a Phillips 500 SEM.

Measurements for specimens are given in millimeters (mm). In the descriptions of new species measurements of antennomeres and body proportions are given as ratios (PL = pronotal length, MPW = width of pronotum at middle, EL = elytral length, MEW = width of elytra at middle). Terms for beetle morphology follow Lawrence and Britton (1991). Naming of wing veins is based on the comprehensive study by Kukalova-Peck and Lawrence (1993). Terms for male genitalia follow Sharp and Muir (1912) and Woodroffe and Coombs (1962), while terms for microsculpture of the cuticle follow Harris (1979). Body setation, as mentioned in the taxonomic descriptions, is based on that condition present on the elytron. Analyses of gut contents for establishing diet follow Leschen (1993).

Method for cladistic analysis is discussed under the section Cladistic Methods.

The taxonomic sections include information that is more or less standard for taxonomic descriptions. Under Diet, personal observations are based on observations of the dissections. Listed in the material examined (Appendix) are all types seen, identified material, and dissected material. For species mentioned in the discussions that follow, in the figure captions, and included in the material examined, the authors' names are listed in the Appendix. Because many Holarctic atomariine genera have been studied recently by Colin Johnson, types of these were not studied.

Public and private collections that contributed material for this project, abbreviations used elsewhere in this paper for collections, and the individuals responsible for the loans are as follows: Albert Allen Collection, Boise, Idaho; American Museum of Natural History, New York (L.H. Herman), Australian National Insect Collection, CSIRO, Canberra (ANIC, J.F. Lawrence); Biological Laboratory, Fukui University, Fukui (H. Sasaji); California Academy of Sciences, San Francisco (R. Brett); Canadian Museum of Nature, Ottawa (CMN, R. Anderson, F. Genier); Canadian National Collection, Ottawa (Y. Bousquet, M. Campbell); J. L. Carr Collection, Calgary, Alberta; Roy A. Crowson Collection, Glasgow; Field Museum of Natural History, Chicago (FMNH, A. F. Newton, Jr.); Instituut voor Taxonomische Zoölogie, Amsterdam (ITZA, C.V. Nidek); Florida State Collection of Arthropods (P. Skelley); Hungarian Natural History Museum, Zoology Department, Budapest (O. Merkl); Richard A. B. Leschen Collection, East Lansing (RALC); The Manchester Museum, Manchester (MANC, C. Johnson); Moscow University Zoological Museum, Moscow (G. Ljubarsky); Musée Royal de l'Afrique Centrale, Tervuren (MRAC, H. André); Museo Argentino de Ciencias Naturales, Buenos Aires (A. Roig Alsina); Museum of Comparative Zoology, Harvard University, Cambridge (MCZ, P. Perkins, S. R. Shaw); Muséum d'Histoire Naturelle, Geneva (MHNG, I. Löbl); Muséum d'Histoire Naturelle, Paris (PARI, N. Berti); Museum of New Zealand Te Papa Tongarewa, Wellington (L. R. Palma); Museum of Zoology and Entomology, Lund University, Lund (R. Danielsson); The Natural History Museum, London (BMNH, M. Kerley); Naturhistorika Riksmuseet, Stockholm (P. Lindskog); Naturhistorisches Museum, Vienna (H. Schönmann); New Zealand Arthropod Collection, Aukland (R. Craw); Orma J. Smith Museum of Natural History, Caldwell, Idaho (ORMA, W.C. Clark); Polish Academy of Sciences, Institute of Zoology, Warsaw (A. Slipiński); Snow Entomological Museum, Lawrence (SEMC, S. Ashe); Karl Stephan Collection, Red Oak, Oklahoma; United States Museum of Natural History, Washington, D.C. (G. House, J. Pakaluk, P. Spangler), Zoological Institute, Academy of Sciences, St. Petersburg (A. Kirejtshuk).

Chilean specimens borrowed from CMN that were collected by S. and J. Peck during 1984-85 and are designated as primary types by me are deposited in the Collecion Nacional de Insectos, Santiago (CNIS).

PHYLOGENETIC ANALYSIS

Monophyly and Relationships of Cryptophagidae: In their influential studies of Cucujoidea, Crowson and Sen Gupta (1955, 1967, 1968a, 1968b, 1969a, 1969b, 1971) recognized that numerous taxa previously included in the Cryptophagidae should be removed and placed in Languriidae. They recognized two adult characters used in combination that separate the Cryptophagidae from other members of the Cucujoidea: the incomplete epipleuron, which extends to the posterior edge of the metasternum (character A, Figs. 138, 149), and the length of ventrite 1, which is longer than the other ventrites (character B, Figs. 79, 149, 179). These characters, however, occur among other groups of the lower Cucujoidea and may not be evidence for monophyly of the Cryptophagidae. Character A is present in *Hobartius* and *Hydnobioides* (Hobartiidae) and character B occurs in *Myriabolia* (Phloeostichidae). These characters, moreover, are absent from a few species of Cryptophagidae. Another character that is perhaps a stronger indication of monophyly is the lateral closure of the mesocoxa by the metasternum (Lawrence 1982, Lawrence and Britton 1991; Figs. 67, 73, 74, 149-151). This character is unusual among the lower cucujoids although it occurs in some members of the Cerylonid series and the langurioid complex (consisting of Languriidae and Erotylidae).

Characters taken from larval morphology that may be useful in defining the cryptophagids were given by Lawrence (1991); however, these are not unique to cryptophagids, occurring in other members of the lower Cucujoidea. The characters of Cryptophagidae and their occurrence in other families, based on the descriptions by Lawrence (1991), are as follows: ventral epicranial ridge absent [Nitidulidae, Cucujidae (*sensu lato*), Phalacridae, Languriidae (except Toraminae and Cryptophilinae), some Erotylidae]; narrow based hyaline prostheca [Sphindidae, Monotomidae, Phloeostichidae, Hobartiidae, Cucujidae (*sensu lato*), Helotidae, Languriidae, Erotylidae]; falciform mala [Monotomidae, Boganiidae, Cucujidae (*sensu lato*), Hobartiidae, Cavognathidae, Languriidae, Erotylidae]; two tarsungular setae [Phloeostichidae, Boganiidae, Hobartiidae, Cucujidae (*sensu lato*), Cavognathidae, Languriidae, Erotylidae]; 1-segmented labial palps (Nitidulidae, Hobartiidae); annular spiracles present in members of the Cryptophaginae [Sphindidae, Cucujidae, Erotylidae (Erotylinae)]. The 1-segmented labial palp is present only among members of Atomariinae and Hobartiidae, which suggests a close relationship between Cryptophagidae and Hobartiidae. Based on a combination of the adult and larval characters described above, I assume that the Cryptophagidae are monophyletic although a more thorough analysis of the lower Cucujoidea is necessary to test this assumption.

Because the characters that "define" the cryptophagids

are widespread and possibly plesiomorphic and the relationships among the lower cucujoids are unknown, the exact sister relationship of the cryptophagids to other members of the lower Cucujoidea is uncertain. Almost every lower cucujoid family has been implicated as a relative of the family Cryptophagidae because of the overall similarity in adult forms among this group. Based on a cursory examination of cucujid-line taxa (see Appendix), I agree with Crowson (1973) that the members of Cavognathidae appear close to Cryptophagidae, especially based on general habitus. Another group that appears similar to the cryptophagids and possibly related, suggested to me by John Lawrence, is Hobartiidae. The members of Cavognathidae and Hobartiidae resemble those of Cryptophagidae by their body form which is a relatively convex shape (not as flattened as that of Cucujidae), pronotum with a lateral pronotal bead (as in Fig. 142), and tentorium without an anterior median process (as in Figs. 13 and 16). The latter feature occurs in many members of the lower Cucujoidea and within the cucujid line a median process of the tentorium is present among members of the Silvanidae, Cucujidae, and Phloeostichidae which suggests that these families may be distantly related to Cryptophagidae. Because of the similarities shared among members of the Cryptophagidae, Hobartiidae, and Cavognathidae, I polarize character states using these families as outgroups. For an additional outgroup to polarize character states, I use members of Cucujidae. Members of these three outgroups, therefore, are used to construct a hypothetical ancestor for rooting the trees in the cladistic analysis. I stress that there are no definitive or uniquely derived synapomorphies that have been identified to unequivocally unite members of Cryptophagidae even though some characters that are similar among Hobartiidae and Cryptophagidae (i.e., form of the epipleuron and larval labial palps) suggest possible relationships.

The inclusion of Alfieriellinae and Hypocoprinae in Cryptophagidae, as supported by Crowson (1980), is questionable. Unlike the remaining Cryptophagidae, the prothorax among members of these subfamilies lacks the lateral carina (Fig. 138), which, in the cucujid line, is characteristic of members currently included in Phloeostichidae. In addition, members of *Alfieriella* (as well as *Amydropa*) have a fused meso- and metasternum (Fig. 150), similar in form to that present in Monotomidae, Silvanidae, and *Hymaea* (Phloeostichidae). However, R. Crowson (personal communication) has persistently argued that the closure of the mesocoxa by the metasternum is reasonable evidence for including these taxa in the analysis. Therefore, I have included Alfieriellinae and Hypocoprinae in the analysis with some reservations.

On the basis of the above discussion of adult characters, there are four genera that should be transferred from the current Cryptophagidae to other families [see list of genera provided by Bousquet (1989) and Johnson and Leschen (in preparation). Members of the Chilean genus *Stengita* Reitter (composed of at least four species, one is described) should be placed in the Languriidae because they lack characters A and B (see above) and have an aedeagus that is oriented vertically in the abdomen and with an elongate strut on the median lobe. These taxa most closely resemble *Toramus* Grouvelle and *Loberoschema* Reitter. The genera *Themephisus* Brèthes (1922) and *Araeostenus* Brèthes (1922), which were described as cryptophagids and later included in Atomariinae by Blackwelder (1945) should be transferred to Phalacridae and Chrysomelidae (Alticinae) respectively.

Terminal Taxa: A well-corroborated phylogenetic hypothesis may be produced if all semaphoronts, fossil taxa, and character sets produced from a variety of methods are included in a cladistic analysis. However, this scientific endeavor is virtually impossible if applied to diverse clades such as Cryptophagidae, given the life span of a researcher, or more realistically, the duration of graduate student tenure! Therefore, to accommodate time constraints, I have chosen a phylogenetic study that can form a basis for further studies of the systematics of Cryptophagidae. I have concentrated on the use of all described genera and taxa exhibiting morphological variation that may contain significant information for cladistic analysis to test current classification schemes and indicate new monophyletic groups.

I have limited this study to adult morphology because larvae are available for only 10% of the included genera (*Antherophagus*, *Micrambe*, *Spavius*, *Cryptophagus*, *Henoticus*, *Atomaria*; plus a few additional taxa that are undescribed [see Taxonomic Treatment]). An analysis that includes larval characters can be done separately to test the phylogenetic relationships proposed in this study. The extinct genera *Cryptophagites* Ponomorenko 1990 and *Nganasania* Zherichnin 1977 are excluded from the analysis because of the uncertainty of their inclusion in the family based on drawings and illustrations in the original publications.

Unfortunately, repeated attempts to locate type specimens of species of *Fratrhenoticus* Bruce 1963 (Cryptophaginae; Madagascar) and *Anathilopus* Falcoz 1921 (uncertain placement; North Africa) and to borrow specimens of *Hypophagus* Ljubarsky 1989 (Atomariinae, probably related to *Hypocoprus* Reitter; Russia) have not been successful. The published descriptions of *Hypophagus* and *Anathilopus* offer little information about characters that can be used for cladistic analysis. Judging from the description and comparative notes made by Bruce (1963) for *Fratrhenoticus*, this taxon is probably a species of *Henoticus*. Most species of *Henoticus* have a 3-segmented antennal club although *Fratrhenoticus* has a two-segmented club. Specimens of some species of *Henoticus* from Africa appear similar to *Fratrhenoticus*; these have a relatively small 9th antennal segment, making the antennal club appear 2-segmented.

Typological definitions for taxa often provide misleading groupings of para- or polyphyletic taxa, whereas definitions that are based on shared derived characters are consistent with monophyletic taxa. Evaluation of the monophyly of genus-level taxa of the Cryptophagidae is based on examination of type material and dissections of specimens that represent a range of variation. Based on these studies, most of the genus-level taxa which were in place before this study

appear monophyletic. Intrageneric problems are discussed in the taxonomic sections.

Taxa (either a single species or group of species) outside the preconceived limits of described genera have been identified as new genera and have been added to the data matrix as terminal taxa. Variations within a genus or putative monophyletic groups of genera are accounted for in phylogenetic analysis by two coding strategies discussed in the next section.

When this study began, there were approximately 41 genera included in the family, most of them well-recognized and established taxa from the northern hemisphere. In this analysis I have included a total of 60 terminal taxa representing most of the described genera and a few undescribed forms. There is complete representation of the genera in the tribes and subfamilies (except those indicated above) except for Cryptosomatulini. There are numerous undescribed species from south temperate regions that belong to Cryptosomatulini, which is a well-defined monophyletic group based on several characters (see below). However, alpha level taxonomic and detailed phylogenetic studies for determining limits of these taxa are necessary. Therefore I have included mainly described cryptosomatuline taxa (two undescribed species were included), represented in the data matrix as species or groups of species that represent genera. Genera included in Cryptophagidae and their placement in tribes and superfamilies are given in the Appendix.

Cladistic Methods: Characters enumerated for phylogenetic analysis (see next section) were coded and entered into a data matrix using MacClade version 3 (Maddison and Maddison 1993). Characters that are polymorphic were entered as 1/0 in the data matrix (see below). A (?) was used to designate unknown character states. Characters that are variable in the outgroup were also coded as a (?) in the hypothetical ancestor (see below). The data matrix was imported to PAUP version 3.1.1 (Swofford 1993). Multistate characters were unordered, except where noted in the character analysis (see character 34), and were assigned equal weights. In PAUP the heuristic tree-building algorithm was used and included the following settings: branch swapping on all starting trees, even nonminimal ones; simple addition sequence; branch swapping with steepest descent. Because of the computer's limited memory, the maximum number of trees stored was 500 and search for multiple islands of trees (Maddison 1991) which implements the random addition sequence could not be done. Another alternative to the random search for locating islands is to specify a different reference taxon in PAUP in the addition sequence prior to tree searching: This was done twice due to time limitations where taxa from different ends of the tree were specified. Strict consensus trees were constructed from the resultant equally parsimonious cladograms. Successive approximations character weighting (Farris 1969), an *a posteriori* character weighting method that bases character weights on the information content of each character in the context of the cladograms produced, was used to produce further resolved cladograms. Character state distribution among cladograms was examined using MacClade. Characters were mapped onto cladograms using ACCTRAN character optimization that reconstructs ambiguous character tracings with accelerated changes toward the root and maximizes reversals (Farris 1970; Swofford and Maddison 1987). Cladistic and character analyses were performed on a Macintosh LC 475.

Variation within a genus or terminal taxon can be represented in a data matrix using two strategies. One strategy is to code the taxon as polymorphic (= more than one character state in a terminal taxon) for the characters observed. I chose this strategy most often and, thereby, implicitly assumed that the variable genera are monophyletic. For example this was done for the genus *Cryptophagus* a genus containing over 200 species and forms. Its monophyly is uncertain in that there is no unreversed and unique synapomorphy for the genus. Moreover, there has been repeated HWL among its members and there is extraordinary variation in the pronotal characters. Another strategy is to include all variants as terminal taxa (see recent papers by Nixon and Davis [1991] and Maddison [1993]). This is a reasonable method because polymorphisms coded in data matrices are not recognized effectively by tree building algorithms in computer programs and, therefore, have no effect in the resultant topologies. The second strategy has been followed for a group of south temperate Atomariinae ("*Chilatomaria*" group, representing those taxa that are glabrous or subglabrous, and the *Atomaria australis* group, representing those species that are heavily punctate).

Because of the ambiguity of relationships among the lower cucujoids, I have created a hypothetical generalized ancestor based on Cucujidae, Hobartiidae, and Cavognathidae to polarize the characters for cladistic analysis. Any character that has more than one state in this hypothetical ancestor is indicated in the matrix by a (?), except where noted in the character analysis (there is a total of 19 characters treated in this way). The polarization of such a character is, of course, unresolved and I allow the parsimony analysis to indicate the groundstate by letting this character perform with the others in the analysis.

Character Analysis: The characters listed below are those that have been identified as potentially informative for cladistic analysis. Polarization of character states, *a priori*, by outgroup comparison (Watrous & Wheeler 1981; Maddison et al. 1984; Nixon and Carpenter 1994) is based on the hypothetical outgroup. Comments made about some characters consider character state distributions among Cucujoidea. The majority of characters are morphological but the last two in the list are behavioral. Characters are numbered and correspond to those in the Data Matrix (Table 1), Results, and Figs. 3-6. Character states that are hypothesized as plesiomorphic (0) are listed first followed by those that are hypothesized as apomorphic (1 - n). States of multistate characters are listed in arbitrary sequence.

For terminal taxa containing both winged and HWL forms, characters associated with the hind wing are coded as they occur in fully winged members. For taxa that are

Table 1. Data matrix used for cladistic analyses of Cryptophagidae. An asterisk (*) indicates a polymorphism (see Character Analysis for multiple states present in taxa). NZ = New Zealand.

	1	2	3	4	5	6
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
Antherophagus	0000000000	0000100000	10*0010000	0000001010	00001100*0	1001011000
Asternodea	0000000002	0000100000	1101010200	1002000010	0011110000	1100011101
Catopochrotus	0000100001	0000100000	1100000000	1100001000	0000110000	1001011000
Cryptophagus	000000000*	0000100000	*0*0010000	000*0010*0	*000110010	*001011000
Henoticus	0000000002	0000100000	1000010200	0002000011	0000110000	0010011000
Henotiderus	0000000003	0000000000	1001010200	0102100011	0000110010	3010011100
Henotimorphus	0000000003	0000100000	1000010000	0002100011	0000110000	2001011000
Genus 1 (Africa)	000000000?	0?00100000	0?0?000???	1010000010	0000?100??	?0???0?0000
Micrambe	0000000003	0000100000	*000010*00	0002001010	*000110000	100001*000
Mnionomidius	0000000003	0000100000	1011010000	0002000000	0000110000	3000001000
Mnioticus	0000000003	0000100000	0000010200	0000000011	*000110000	10*0001000
Myrmedophila	0000000003	0000100000	1000010000	0000001010	0000110010	2000011000
Neohenoticus	0000000002	0000100000	1000010200	0002100011	0000110000	3010011000
Paramecosoma	0000000003	0000100000	0000010000	0003001000	1000110010	3001011000
Pteryngium	0000000002	0000100000	1000010200	0002000010	0000110000	0010001000
Salebius	0000000003	0000100000	1000010300	0003001010	1000110010	3001011000
Serratomaria	0000000002	0000100*00	0000010200	0002100010	0000110000	3100011100
Spaniophaenus	0000100003	0000100000	1000010000	0100001000	0000110010	1001011000
Spavius	0000000003	0000100000	1000010000	0100001000	0000110010	1001011000
Striatocryptus	0101000002	0000100000	0001010200	001*00*010	0000110000	**1001110*
Telmatophilus	0000000002	0000100000	0000010200	0002000011	0000110010	0000011000
Agnetaria	0000020002	0000100000	1000110000	0000000200	0000110001	0000001000
Antarcticotectus	0000000002	0000100000	0000111000	0000000200	0000110001	0001001000
Brounina	0000000002	0000100000	1000111000	0000000100	0001110001	0001001000
Chiliotis	0000000002	0000100000	1000111000	0001000200	0000110001	0000001000
C. gibbipennis	0000000002	0000100000	1001110000	0004000*00	0001110001	0001001000
C. tasmanicus	0000000002	0000100000	1000010000	0000002100	0000110001	0001000000
Cryptothelypterus	0000000002	0000100000	1000010000	0004000000	0000110001	0001000000
Micrambina (Chile)	0000000002	0000100000	1000111000	2001000100	0001110001	0000001000
Neopicrotus	0100020002	0000010000	1011011000	0000000000	0000110001	0000001001
Micrambina (NZ)	0000000002	0000100000	1000111000	2000000000	0001110000	000*001000
Picrotus	0100020012	0000110000	1011000000	0000000000	0001110001	000100*001
Genus 2 (NZ)	0100000002	0000100000	1001011000	0000000000	0001110001	0001001000
Thortus	0100000012	0000110000	1011010000	0000000000	0001110001	0001001000
Caenoscelis	0000000002	1010111000	1100010000	0000000000	0*01110000	0001001000
Dernostea	0000011000	1010011000	1100010000	1000000000	0111111100	000?001001
Himascelis	0000020000	1010111010	1100010000	1000000000	0111111100	0000001101
Sternodea	0000020000	1010111000	1100010000	1000000000	0111110000	0000001000
Atomaria	0*00000*02	0110*01110	0100000101	0000000000	0000000010	1000001000
A. australis	0000000102	01101001*0	010*000101	0000000000	000*000000	100000100*
Atomaroides	0000000100	0010000100	0100000101	0000000000	0000000010	1000000001
Curelius	1100001101	0110000100	0100000101	1000000000	0100010010	1000000001
Chilatomaria	0000000002	0110100100	0100000101	0000000000	0001000000	1000001001
Ephistemus	110000110*	01100001*0	0100000101	1000000000	0100010010	1000000001
Microatomaria	0000020002	0110000100	0100000101	0000000000	0001000000	1000001001
Ootypus	1000000102	0110001110	0100000101	1000000000	0000010010	1000000000
Paratomaria	0000000102	0110101110	0100000101	0000000000	0001000000	1000001000
Salltius	0000000102	0111001110	0101001101	0000000000	0001000000	1000001001
Tisactia	0100001001	0110000100	0100000101	1000000000	0100010010	1000000001
Cryptafricus	0111020000	0111000100	0101000011	0000000000	0000100000	0000000000
Cryptogasterus	0100000000	0111000101	0000010111	0000022000	0001100000	1000000001
Anitamaria	0*01000000	0111000101	000*010111	000002*000	0001100000	1000000001
Microphagus	0101000003	0111000101	0001000111	0000002000	0001100000	1000000001
Alfieriella	0011010002	0000100000	1010000010	0000010000	0001000000	0000100010
Amydropa	0010000002	0000000000	0110000010	0000010000	0001000000	0000100010
Hypocoprus	0000000002	0010000000	0110000010	0000010000	0000010000	0000100000
Ancestor	0?0?000000?	000??00?0?	??000??000	0000000000	00000?0000	000000?000

Table 1. (Continued).

	7	8	9	100	1	
	1234567890	1234567890	1234567890	1234567890	1234567890	1234
Antherophagus	0001210***	00000001*2	1000000000	0000000000	**00001000	0011
Asternodea	0000410110	0000000122	1000020000	0000020000	0000111000	0000
Catopochrotus	0000410000	0000000112	100000???0	0000000000	0000001000	0022
Cryptophagus	0001*1001*	10*00001*2	1000000000	0000000000	0*0000*000	000*
Henoticus	0001310010	00*0000102	100001000*	0000000000	0*0001*000	0000
Henotiderus	0000310011	1000000012	1000010000	00000000*0	0000101000	0000
Henotimorphus	0001310011	1000000112	100000???0	0000000000	0000011000	0000
Genus 1 (Africa)	?00?21000?	?0?00001??	?000??????	?????00000	1?????1000	00??
Micrambe	0001*100**	00*00001*2	1000000000	0000000000	0*000*1000	0000
Mnionomidius	0001310001	1000000122	100002???1	0000000000	01????1000	0020
Mnioticus	00012100**	0010000012	1000020000	0000000000	01????0000	0000
Myrmedophila	0001210011	1000000112	1000000000	0000000000	0000001000	0022
Neohenoticus	0000310011	1000000112	1000020000	0000000000	0000121000	00??
Paramecosoma	0001210001	0000000112	1000000000	0000000000	0000001000	0020
Pteryngium	0001410001	0000000100	0000020000	0000000000	0000021000	0000
Salebius	0001310011	0000000112	1000000000	0000000000	0000001000	0000
Serratomaria	0000310011	0000000021	10000*000?	0000000000	0000111000	0000
Spaniophaenus	0001*100*0	1000000112	1000000000	0000000000	0*00001000	002*
Spavius	0001210001	1000000112	1000000000	0000000000	0000001000	0002
Striatocryptus	0000210011	*0000000*1	1000020000	0100000010	0000*3*001	0020
Telmatophilus	0001*10011	0000000112	1000020000	0000000000	0000110000	0110
Agnetaria	0000310000	0000000100	0000100001	0000000000	0000011010	0020
Antarcticotectus	0001310000	0000000100	0000100001	0000000000	0000011000	0000
Brounina	0001310000	0000000100	0010100001	0000000000	0000041010	00??
Chiliotis	0001310000	0000000100	0000100001	0000000*00	0000051000	0000
C. gibbipennis	0001310000	0000001100	0000100001	0000000000	0000011010	0000
C. tasmanicus	0000310000	0000000100	0000100001	0000000000	0000051010	0000
Cryptothelypterus	0001310000	0010000100	0000100001	0000000000	01????1010	0030
Micrambina (Chile)	0001310000	0000000100	0010100001	0000000100	0000051010	0000
Neopicrotus	0001310100	0010000100	0000000001	0000000000	01????1010	00?0
Micrambina (NZ)	0001310000	0000001100	000010000*	0000000*00	0000031010	0000
Picrotus	0001410100	0010010100	0000000001	0000000001	01????1010	0000
Genus 2 (NZ)	0001310000	0010000100	0000000001	0000000000	01????1010	0000
Thortus	0000310100	0010001100	0000000001	0000000000	01????1010	0000
Caenoscelis	0001*10000	0000001100	0002000000	0000020000	0*0006*010	0000
Dernostea	0001410100	0010000100	0002000002	?????20000	01????1010	00??
Himascelis	0001410100	0010001100	0002000000	000?120000	01????1010	00?0
Sternodea	0001410000	0010001100	0002000000	0000120000	01????1010	00?0
Atomaria	1010*1*000	1000000121	200002*001	0110100000	0*0*040000	0000
A. australis	*010210000	1000001121	20000**001	0110100000	0*00010000	00*0
Atomaroides	1010210000	1000000101	100003???1	0110100000	0001062000	00?0
Curelius	1010410100	1000010121	2000020001	0110100000	0001050000	0000
Chilatomaria	2010210000	1000000121	2000021001	0110100000	0000010000	0000
Ephistemus	1010410100	1000010121	2000020001	0110100000	0001050000	0000
Microatomaria	2010310100	1000001121	2000001001	0110100000	0000060000	0000
Ootypus	1010310100	1000000121	2000020001	0110100000	0001050000	0000
Paratomaria	1010210000	1000001121	2000000001	0110100000	0000030000	0110
Salltius	2010210*00	1000000121	200000100?	0111100000	0000050000	0100
Tisactia	1010410100	1000010121	200002000?	0110100000	*001050000	0000
Cryptafricus	0100110100	0000010100	000102????	???0100000	0001062101	0000
Cryptogasterus	0010211100	0101010101	3101030110	1111011000	1011060101	1000
Anitamaria	0*1021**00	1101010101	310103011*	111*0*1000	*011060001	1000
Microphagus	0000111*00	1001000101	2101000110	1111000000	1001060101	1000
Alfieriella	0100210100	0020*00100	000001000?	0000000001	01????0001	1020
Amydropa	0100110100	0020*00100	0000041002	0000010001	01????0101	0000
Hypocoprus	0000310100	0000010000	0000011000	0110000000	0001060001	1002
Ancestor	0000?00000	0000000000	0000000000	0?00?00000	?0000??000	0000

brachypterous or apterous, these characters are coded as unknown and are designated with a (?) in the data matrix.

1. *Body form.* (0) Elongate; (1) oval. Most members of the Cryptophagidae are elongate and somewhat parallel-sided (e.g., Figs. 176-207); however, a few are oval or round (*Ephistemus*, *Curelius*, and *Ootypus*, as in Fig. 208). "Roundness" of a beetle is actually defined by a suite of characters (e.g., higher pronotal volume, convexity of the pronotum and elytra, changes in the proportions of individual segments and sclerites) that contribute to the overall shape of the beetle. Because these characters covary, I codified body shape which represents the entire suite of characters. State 1 is absent from members of the outgroup and, therefore, it is hypothesized as apomorphic.

2. *Punctation in the prosternal area.* (0) Present; (1) absent. Well-defined punctures are distributed over the entire body of most Cryptophagidae and the outgroup (except for one species of *Hobartius*). Punctures are absent in the prosternal region among members of the Picrotini (Fig. 135), Ephistemini, and *Striatocryptus*. Because both states occur in members of the outgroup the polarity of this character is uncertain. This character is coded as polymorphic for *Atomaria* and *Anitamaria*.

3. *Alveolate punctation.* (0) Absent; (1) present. Punctation on the body of Cryptophagidae and the outgroup consists of circular or oval (in some species of *Cryptophagus*, *Micrambe*, and *Asternodea*) punctures that bear setae (as in Fig. 145). Alveolate punctation is present in species of *Alfieriella* and *Amydropa* (Fig. 93) and is clearly visible on specimens treated in KOH. State 0 is present in the outgroup and is hypothesized to be plesiomorphic.

4. *Length of the terminal antennomere.* (0) Subequal to that of the penultimate antennomere; (1) 2x the length of the penultimate antennomere. Among most species of Cryptophagidae and the outgroup, the length of the terminal antennomere is more or less equal to that of the preceding antennomere. In *Striatocryptus* (Fig. 26), some atomariines (Fig. 23), and some members of the outgroup, the terminal antennomere is approximately 2x the length of the preceding antennomere. Because state 1 occurs in some members of the outgroup the polarity of this character is uncertain.

5. *Form of terminal antennomere.* (0) Asymmetrical and slightly compressed; (1) symmetrical and more or less flattened. The terminal antennomere is asymmetrical in shape among most members of the outgroup and Cryptophagidae; however, its shape in *Catopochrotus* and *Spaniophaenus* is symmetrical (Fig. 33). State 1 is absent in members of the outgroup and it is therefore hypothesized as derived.

6. *Antennal club.* (0) 3-segmented; (1) 2-segmented; (2) 1-segmented. State 1 is present in *Agnetaria*, some species of Picrotini, some atomariines (Figs. 22, 27) and Caenoscelini. State 2 is present in species of *Alfieriella* (Fig. 28) and some caenoscelines (Fig. 31). State 0 is present in members of the outgroup and it is hypothesized as plesiomorphic.

7. *Third antennomere.* (0) Up to 2x the length of the antennomere 4; (1) at least 3x the length of the antennomere 4. Antennomere 3 among most species of Cryptophagidae and the outgroup is equal or subequal in length to that of the remaining antennomeres. In contrast, the length of the antennomere 3 in *Dernostea* (Fig. 31) and Ephistemini is 3x the length of the remaining antennomeres. State 0 is present in the outgroup and it is hypothesized as plesiomorphic.

8. *Shape of funicle.* (0) Cylindrical; (1) conical and curved. Among the outgroup and most cryptophagids, the funicle is typically parallel-sided with the basal articulating stem arising from a subapical position along its base. In contrast, the funicle of some atomariines is not parallel, but curved (Fig. 30), and the sides converge towards the base of the articulating stem forming a "lopsided" cone. State 1 is present only among some Atomariinae and it is hypothesized as apomorphic. This character is coded as polymorphic for *Atomaria*.

9. *Antennal insertion.* (0) Into a concavity smaller than the diameter of the funicle; (1) into a concavity equal to or larger than the diameter of the funicle. The antenna is inserted into a large concavity among some members of the Picrotini (Fig. 132). In contrast, the antenna is inserted into a small concavity or slight depression among the remaining members of the Cryptophagidae and the outgroup. Because state 0 is present in the outgroup, it is, therefore, hypothesized as plesiomorphic.

10. *Number of tubercles present on the dorsal surface of the right mandible.* (0) 0; (1) 1; (2) 2; (3) 3. The number of tubercles on the dorsal surface of the mandibles varies considerably among species of Cryptophagidae (Figs. 17-20, 164). Examination of the number for each mandible indicates that it varies inconsistently within genera and species for the left mandible; in contrast, the number of tubercles of the right mandible is consistent. Therefore, the number of tubercles present for the right mandible is enumerated for this character. When a multiple number of tubercles are present it is easy to distinguish them into basal and distal based upon their relative distribution on the surface of the mandible. However, when one tubercle is present (e.g., among members of the Atomariinae), it is difficult to decide if this is homologous to the basal or distal tubercle of other members of the cryptophagids. Therefore, only the number of tubercles is used as a character in this study.

The number of tubercles present in the groundplan of the cryptophagids is equivocal because they number either 0 or 2 in the outgroup. This character is coded as polymorphic for *Cryptophagus* (states 2 and 3) and *Ephistemus* (states 0 and 1).

11. *Serrations on the incisor lobe of the mandible.* (0) Absent; (1) present. Among Caenoscelini (Figs. 18, 167) there are serrations present on the cutting edge of the incisor lobe of the left mandible (most genera) or on both mandibles (*Caenoscelis*). These serrations are absent from the mandible of the remaining Cryptophagidae. Because state 0 is present in the outgroup it is hypothesized as plesiomorphic.

12. *Sensory pores on the basal portion of the mandible.* (0) Absent; (1) present. A field of sensory pores is present on the mandible (Figs. 20, 164) among most species of Atomariinae (with the exception of *Atomaroides*); in contrast, they are absent among the remaining Cryptophagidae. State 0 is present in the outgroup and it is hypothesized as plesiomorphic.

13. *Width of labial palpomere 1.* (0) Subequal to that of palpomere 2; (1) greater than that of palpomere 2. Among Cryptophagini and Cryptosomatulini the width of palpomere 1 is subequal to that of palpomere 2 (terminal palpomere, Fig. 127). Also among these groups, the length of palpomere 1 is shorter than palpomere 2. In contrast, among species of Caenoscelini (Fig. 130) and Atomariinae (Figs. 126, 129), palpomere 1 is wide and often longer than palpomere 2. State 0 is present in the outgroup and it is hypothesized as plesiomorphic.

14. *Median process of the mentum.* (0) Present; (1) absent. The anterior margin of the mentum may have a median and two lateral processes. Most species of Cryptophagidae have the median process (Figs. 127, 130); however, it is absent among some species of Atomariinae (Figs. 125, 129) and Cucujidae and *Hobartius* of the outgroup. Because both states are present in the outgroup polarity of this character is uncertain.

15. *Transverse ridge or line on mentum.* (0) Absent; (1) present. The

mentum may have a transverse line (Fig. 127) or ridge that marks an angle behind the palpal insertions on the surface of the mentum. This feature is widespread among Cryptophagidae and is variable in the outgroups. State 0 is present among some species of Atomariinae (Figs. 126, 129), *Dernostea*, *Hypocoprus*, and Alfierielinae (Fig. 125). Because both states of this character are present among members of the outgroup its polarity is equivocal. This character is coded as polymorphic for *Atomaria*.

16. *Ridge surrounding antennal concavity.* (0) Absent; (1) present. Among species of Caenoscelini and Picrotini, the antenna inserts into a well-developed antennal concavity (Fig. 132) at the front of the head. The dorsal margin of the concavity is surrounded by a distinct ridge or bead slightly concealing the antennal insertion. State 0 is present in the outgroup and is, therefore, hypothesized to be plesiomorphic.

17. *Boss on front of head.* (0) Absent; (1) present. A small triangulate boss may be present above the space between the antennal insertions on the frons (Fig. 133). This is present on those cryptophagids that have the antennal insertions approximate (Caenoscelini and some Atomariinae). This structure should not be confused with a distinct carina that separates the antennal insertions on the frons in *Thortus* (Fig. 132). Because state 0 is present in the outgroups, it is, therefore, inferred as plesiomorphic.

18. *Frontoclypeal suture.* (0) Absent; (1) present. A distinct frontoclypeal suture is present among some Atomariinae (Fig. 133), one species of *Serratomaria*, and *Hobartius*. The widespread absence of this character among members of Cryptophagidae and its presence in part of the outgroup suggests that state 0 may be plesiomorphic. However, until resolution of the phylogenetic relationships of the outgroup is established, the polarity of this character is ambiguous. This character is coded as polymorphic for *Serratomaria*.

19. *Clypeus.* (0) On same plane as that of the frons; (1) on lower plane than that of frons. The clypeus is on a lower plane than the frons (Fig. 133) in some species of Atomariinae (both states occur among *Ephistemus* and *Atomaria australis* group). State 0 (Fig.

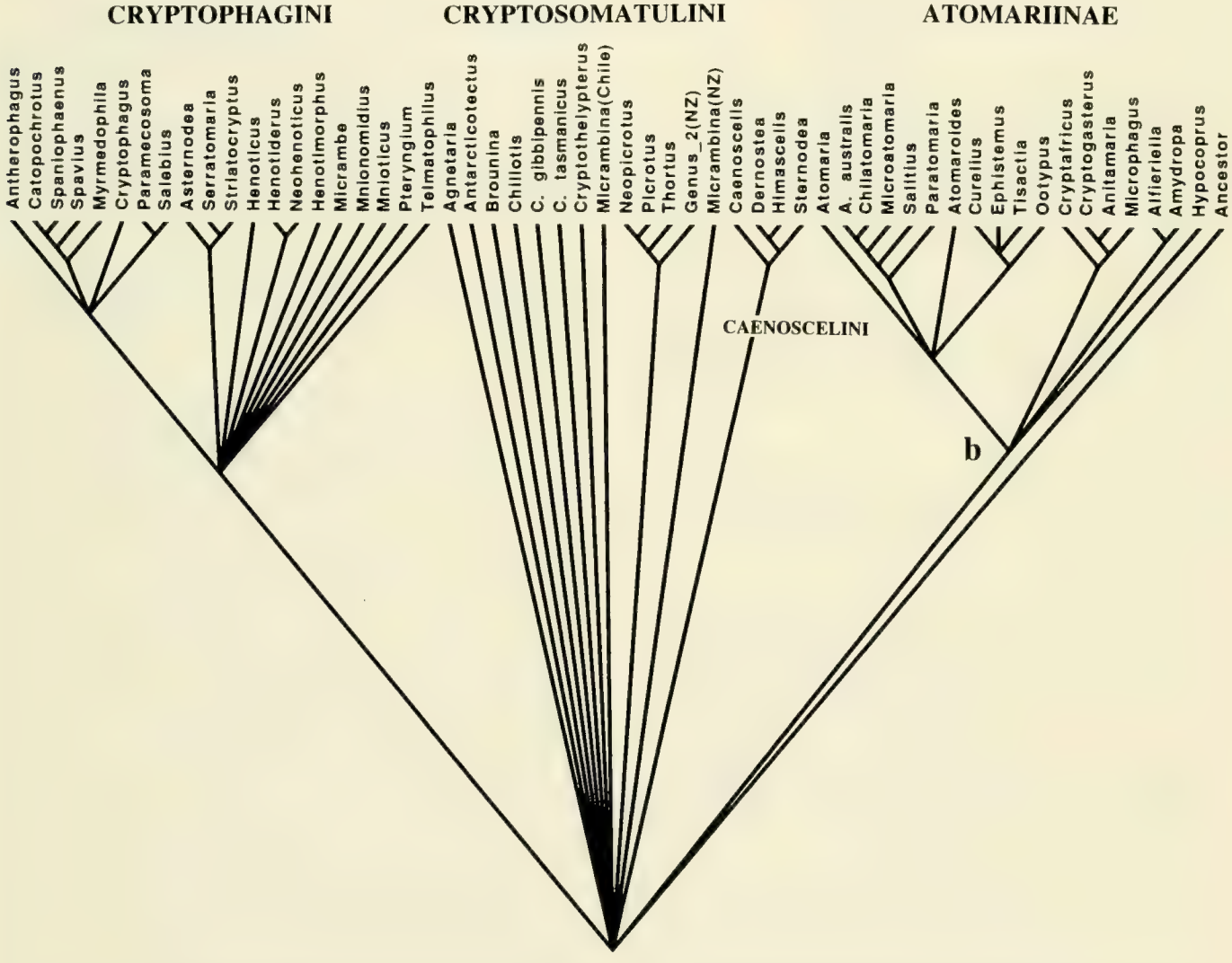


Fig. 1. Strict consensus tree (of 500 trees) of the phylogenetic relationships among members of Cryptophagidae with equal weighting of characters.

134) is present in the outgroup and it is hypothesized as plesiomorphic. This character is coded as polymorphic for *Chilatomaria* and *Ephistemus*.

20. *Tubercle on margin of frons.* (0) Absent; (1) present. Among some species of Atomariinae there is a tubercle on the lateral portion of the frons below the antenna (Figs. 13, 165). State 1 is present among Hobartiidae and, therefore, the polarity of this character is uncertain.

21. *Subgenal spine.* (0) Poorly developed or absent; (1) present. A well-defined subgenal spine, located at the base of the mandibular articulation, is present among most species of Cryptophaginae (Figs. 140, 145), *Alfieriella* (Fig. 14), and Cucujidae. Because both states are present in members of the outgroup, the polarity of this character is uncertain. This character is coded as polymorphic for *Cryptophagus* and *Micrambe*.

22. *Gular sutures.* (0) Present; (1) absent. A pair of gular sutures is typically present in the gular region of the head of many beetles (Fig. 16), but these are absent in Caenoscelini, most Atomariinae (Figs. 13, 136), *Amydropa*, *Hypocoprus*, and one specimen of *Hobartius*. State 0 is widespread among members of the outgroup and most Cryptophagidae and its polarity is equivocal.

23. *Eyes.* (0) Well developed; (1) reduced to a fewer number of facets. The "normal" number of eye facets (when counted from dorsal view at the greatest length of the eye) of most members of the Cryptophagidae and the outgroup varies from 10-20. Reduction of the eyes to a smaller number of facets occurs in some species of *Cryptophagus*, *Antherophagus*, *Alfieriella*, *Amydropa* (Fig. 128), *Hypocoprus*, *Mnionomidius*, and Picrotini (Fig. 132). Among these taxa the number of facets range from 3-6. State 0 is present in the outgroup and it is hypothesized as plesiomorphic. This character is coded as polymorphic for *Antherophagus* and *Cryptophagus*.

24. *Ocular setae.* (0) Present; (1) absent. Simple setae are distributed between the eye facets and are present in most species of Cryptophagidae. The ocular setae are absent in a few species of Cryptophaginae and Atomariinae. State 0 is present in the outgroup and it is hypothesized as plesiomorphic. This character is coded as polymorphic for members of the *A. australis* group and *Anitamaria*.

25. *Temporal ridge.* (0) Absent; (1) present. A distinct temporal ridge located behind the eye (in dorsal view) is present among some species of Cryptosomatulini (Fig. 16). This ridge is absent among the remaining members of Cryptophagidae and the outgroup and, therefore, state 1 is hypothesized as apomorphic.

26. *Line on the vertex of the head.* (0) Absent; (1) present. A distinct transverse line on the vertex of the head and behind the eye is present among Cryptophaginae (Figs. 132, 140, 148), a few Atomariinae, and Cucujidae. This line is absent among most members of Atomariinae (Figs. 131, 134). Because state 1 occurs in part of the outgroup, polarity of this character is uncertain.

27. *Head.* (0) Not constricted behind the eye; (1) constricted behind eye. Among some species of Cryptosomatulini (Fig. 16), Picrotini, and *Salltius*, the head is constricted behind the eye forming a broad neck. Because state 1 is present in part of the outgroup the polarity of this character is ambiguous.

28. *Cephalic glandular ducts.* (0) Absent; (1) present on inside margin of antennal insertion; (2) present and well developed on outside margin of antennal insertion; (3) present and poorly developed on outside margin of antennal insertion. Two glandular ducts that open either onto the clypeal region near the inside margin of the antennal insertion (Figs. 13, 133, 159, 160) or onto the preocular region of the frons near the outside margin of the antennal insertion (Fig. 166) are present among members of the Atomariinae and Cryptophaginae, respectively. In members of *Salltius*, these ducts are fused into a common duct (Fig. 160). These ducts are absent among members of the outgroup, therefore, state 0 is hypothesized to be plesiomorphic. This character is coded as polymorphic for *Micrambe* (states 0 and 3).

29. *Shape of posterior portion of the tentorium.* (0) A straight transverse bar; (1) a straplike loop. Among some species of Atomariinae the posterior portion of the tentorium is looped and straplike (Fig. 13). This is unlike the barlike form that is present in the remaining species of Cryptophagidae (Fig. 16). State 0 is present in the outgroup and is hypothesized as plesiomorphic.

30. *Anterior arms of the tentorium.* (0) Separate; (1) fused. The anterior arms of the tentorium are fused among species of Atomariinae (Fig. 13) and Caenoscelini: these arms are separate among the remaining Cryptophagidae (Fig. 16). Because state 0 is present in the outgroup it is, therefore, hypothesized as plesiomorphic.

31. *General shape of pronotum.* (0) Parallel-sided or its greatest width at the middle; (1) converging anteriorly, its greatest width at its base (Fig. 45); (2) greatest width in the anterior half (Fig. 44). State 0 occurs among most species of Cryptophagidae, except for a few Cryptophaginae, Ephistemini and most Caenoscelini. I am excluding that width contributed by the angularity and teeth present on the pronotum among some species of Cryptophaginae. State 0 is present in the outgroup and it is hypothesized to be plesiomorphic.

32. *Anterior margin of pronotum.* (0) Straight; (1) emarginate. Among some species of Cryptophaginae the anterior margin of the pronotum is emarginate such that the sides extend beyond the fossa in which the head inserts (Figs. 40, 43, 45). Because state 0 is present in the outgroup it is hypothesized to be plesiomorphic.

33. *Sides of the pronotum.* (0) Not explanate; (1) explanate. Typically the sides of the pronotum among Cryptophagidae are not broadly explanate, except in Genus 1 and *Striatocryptus*. Because state 0 is present in the outgroup it is, therefore, inferred as plesiomorphic.

34 & 35. *Lateral pronotal margin.* (0) Unmodified; (1) grooved; (2) serrate; (3) sinuate; (4) with setiferous tubercles; (5) irregularly serrate. The margin of the cryptophagine pronotum is highly variable. A "grooved" pronotum occurs in some members of the Cryptosomatulini (Fig. 146). Between the marginal bead and a row of setae along the margin there is a wide space and when viewed in normal light, this space looks superficially like a longitudinal groove.

Among many members of the Cryptophagini the pronotal margin is evenly (state 2, Figs. 50-53), or irregularly serrate (state 5, Figs. 54, 147, 145). The former condition exhibits a row of equal sized teeth that are evenly spaced. In contrast, in the latter condition, the teeth are of unequal sizes and are unevenly distributed on the pronotal margin. Because state 2 is more widespread among cryptophagines, and irregular serrations bear strong similarity to state 2, I hypothesize that there is an ordered transformation from state 2 to 5 in the character state tree. The only way to effectively order part of a transformation series is to employ a mixed coding strategy in the character matrix (O'Grady and Deets 1987, Wiley et al. 1991). In the data matrix one column represents states 0-4 (Character 34) and another column (Column 35) represents character state 5 in which a 0 represents states 0-4. Character 35 state 1 is ordered relative to character 34 state 2.

A sinuate or undulate margin that consists of three processes occurs in members of *Paramecosoma* and *Salebius* (Fig. 42), while setiferous tubercles occur on the margin in some Cryptosomatulini (see Figs. 7-10 in Leschen and Lawrence 1991). The margin of the pronotum is somewhat irregular among Hobartiidae. Because states 1-5 are absent among members of the outgroup, these are hypothesized as apomorphic. This character is coded as poly-

morphic for *Cryptophagus* and *Striatocryptus* (states 0 and 2).

36. *Pronotal bead.* (0) Present; (1) absent; (2) present in basal half. The pronotal bead (or carina) is completely absent in members of *Hypocoprus* (Fig. 195), *Alfieriella* (Fig. 196), and *Amydropa* (Figs. 137, 138); and it is present in the basal half in two species of Atomariinae. The pronotal bead is widespread among members of the lower Cucujoidea; however, it is absent in some species of Phloeostichidae. Because a pronotal bead is present in the outgroup, state 0 is hypothesized to be plesiomorphic.

37. *Pronotal angularity.* (0) Absent; (1) present in marginal bead; (2) present above marginal bead. On the anterolateral margin of the pronotum there is a platform (Figs. 140, 143, 148) that has been referred to as an angularity. Its general appearance is variable and has been used as a species character among *Cryptophagus* (see Woodroffe and Coombs 1961). I consider an angularity as present when there is a distinct platform or a widened surface in the anterior part of the marginal bead with associated glandular ducts. This surface is presumably an evaporative surface for secretions from glandular ducts that open on it. State 1 is characteristic of many members of Cryptophagini. A similar feature occurs in some Cryptosomatulini and Atomariinae, however it is not located in the pronotal bead but above it. Among Cryptosomatulini, this angularity is associated with a dense cluster of microtubules (Fig. 162). Also a narrow process or small tubercle that bears a glandular duct occurs in some Atomariinae (Figs. 141, 161). Among atomariines that have this character, there are associated clusters of setae that obscure the tiny process from view. State 0 is present among the outgroup and, therefore, states 1 and 2 are hypothesized as apomorphic. This character is coded as polymorphic for *Striatocryptus* (states 0 and 1) and *Anitamaria* (states 0 and 2).

38. *Depressions on the pronotum.* (0) Absent; (1) paired depressions present at base of pronotal disc; (2) a broad transverse basal impression present. State 1 occurs in Cryptosomatulini and one species of Atomariinae. State 2 occurs in some species of Cryptosomatulini. States 1 and 2 are absent among members of the outgroup and they are hypothesized as apomorphic. This character is coded as polymorphic for the *Cryptophagus gibbipennis* group (states 0 and 1).

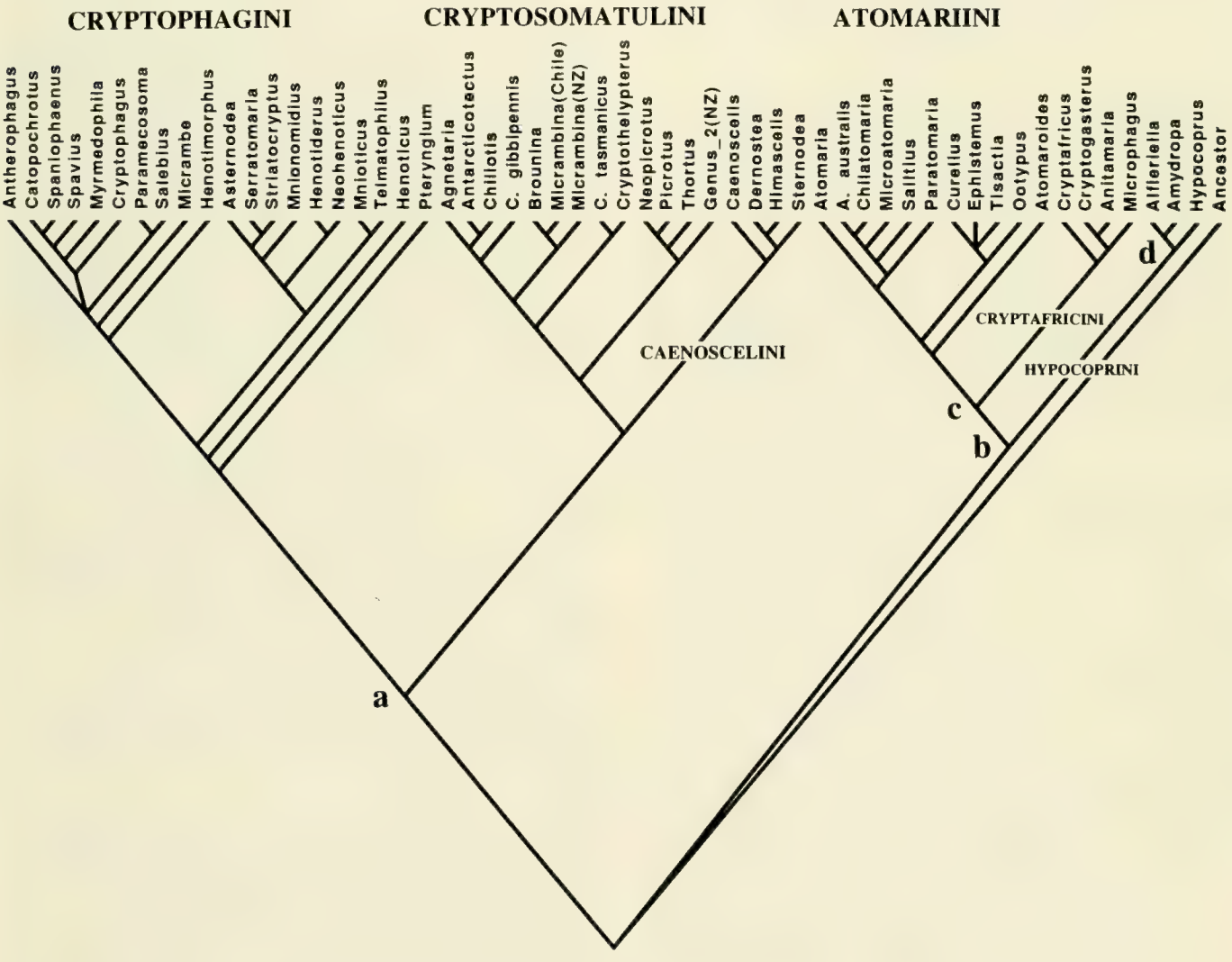


Fig. 2. Strict consensus tree (of nine trees) of the phylogenetic relationships among members of Cryptophagidae with successive approximations weighting of characters.

39. *Basal pits of pronotum.* (0) Absent; (1) present. Among some Cryptophagini there are distinct basal pits or fovea near the basal bead of the pronotum (Figs. 42, 43, 47, 48, 140, 142, 145). These are absent among the outgroup, state 1 is hypothesized as apomorphic. This character is coded as polymorphic for *Cryptophagus.*

40. *Basal pits of pronotum connected by a groove.* (0) Absent; (1) present. State 1 occurs in some species of Cryptophagini (Figs. 42, 43, 47, 48, 142). State 0 is present in the outgroup and it is hypothesized as plesiomorphic.

41. *Median fold.* (0) Absent; (1) present. A short longitudinal line or ridge present in the mid-basal portion of the pronotum occurs in some species of Cryptophagini (Fig. 42). This structure has been named the median fold by Woodroffe and Coombs (1962). State 1 is absent among the outgroup and it is hypothesized as apomorphic. This character is coded as polymorphic for *Cryptophagus, Mnioticus,* and *Micrambe.*

42. *Lines on the prosternal process.* (0) Absent; (1) present. In Ephistemini the prosternal process bears longitudinal lines that flank the prosternal process and end on the anterior region of the prosternum near the openings of paired glandular ducts. Similar lines are present among Caenoscelini (Fig. 36, 144). These lines are absent in the outgroup and, therefore, state 1 is hypothesized as apomorphic.

43. *Prosternal process.* (0) Not vaulted; (1) vaulted. The prosternal process of some Caenoscelini and *Asternodea* is vaulted with the lateral margins more or less perpendicular to the horizontal plane (Figs. 36, 64, 144). Among the remaining Cryptophagidae the prosternal process is smooth and contiguous with the sternal and hypomeral regions. State 0 is present in the outgroup and it is hypothesized as apomorphic.

44. *Notch on hypomeron.* (0) Present; (1) absent. A distinct notch is present on the hypomeron laterad of the procoxal insertion (Figs. 37, 40, 57). This notch may be closed and is present in the form of a short line (Fig. 41). This notch is absent among many cryptophagids (Figs. 36, 39, 46, 56, 58, 59, 63, 64, 135), but is present in most Cryptophagini. State 1 is absent among the outgroup, and numerous other cucujoids, and it is hypothesized as apomorphic. This character is coded as polymorphic for the *A. australis* group.

45. *Internal closure of the procoxal cavity.* (0) Open; (1) closed. In state 0, the coxal cavity is open internally such that the endopleuron is not visible upon removal of a coxa (Figs. 37, 58). An internally closed procoxal cavity is present in Cryptophaginae (Figs. 40, 41, 135) and a few Atomariinae (Fig. 57). State 0 is present in the outgroup and it is hypothesized as plesiomorphic.

46. *External closure of the procoxal cavity.* (0) Partially closed; (1) completely open behind. Traditionally beetle workers consider a closed coxal cavity as that condition where the hind margin of the procoxa is bordered by a flange of the prosternum (e.g., some members of Tenebrionoidea), a flange of the hypopleuron (e.g., numerous beetle groups including some cucujoids), or both in combination (e.g., Sphindidae). Within Cryptophagidae a partially closed procoxal cavity is that condition where the flange of the hypomeron only partially wraps around the procoxa (Figs. 37, 58). This state occurs in Cryptophaginae, a few Atomariinae, *Hypocoprus,* and Cucujidae. Because of the variable distribution of states among the outgroup, polarity of this character is ambiguous.

47. *Deep transverse pits on the prosternum.* (0) Absent; (1) present. Among some Caenoscelini there are transverse pits that open laterally on the prosternum (Figs. 36, 144). Similar pits among other Cucujoidea occur in some species of *Corticaria* (Corticarinae; Latridiidae). State 1 is absent in the outgroup and it is hypothesized as apomorphic.

48. *Antennal grooves on the hypomeron.* (0) Absent; (1) present. Parallel antennal grooves on the hypomeron are present among some species of Caenoscelini (Figs. 36, 144). State 0 is present in the outgroup and it is hypothesized to be plesiomorphic.

49. *Two glandular ducts in the anterior portion of the prosternum.* (0) Absent; (1) present. State 1 occurs in some Cryptophagini (Fig. 40) and Atomariinae. These glandular ducts are absent among the outgroup and, therefore, state 1 is hypothesized as apomorphic. This character is coded as polymorphic for *Antherophagus.*

50. *Microtubules.* (0) Absent; (1) present. Clusters of sclerotized microglandular ducts, termed here microtubules (see Crowson [1990] for a similar feature present in Boganiidae). These are present among members of the Cryptosomatulini (Fig. 162) and Picrotini, are smaller in diameter (less than 0.001 mm) than those sclerotized glandular ducts among other members of the Cryptophagidae (about 0.003 mm or more). These ducts, observed in cleared specimens, are present mainly in the thorax, but may occur in other regions as well (e.g., sternal regions). They are usually associated with the base of setae and may in fact be associated with cells that contribute to the formation of the setae. State 0 is present in the outgroup and it is hypothesized as plesiomorphic.

51. *Glandular ducts opening onto the lateral margin of the pronotum.* (0) Absent; (1) 1 duct; (2) 2 ducts; (3) 3 or more ducts. A single glandular duct is present among most Cryptophagini and Atomariinae. The number of glandular ducts that open onto the lateral margin of the pronotum varies among Cryptophagini (Figs. 40, 49-54). There are up to three (or more in members of *Mnionomidius* [Fig. 52] and *Neohenoticus* [Fig. 54]) ducts that can be recognized based upon their relative positions on the margin of the pronotum; anterior, middle, and posterior. However, it is difficult to determine which glandular duct present in Cryptophagini is homologous to the single duct present among Atomariinae. Determination of homology would be easy if the glandular ducts were consistent in their location among atomariines; but, they may occur either in the anterior or in the middle of the pronotum. Glandular ducts are present only in Cryptophagidae and, therefore, state 0 is hypothesized as plesiomorphic. This character is coded as polymorphic for *Cryptophagus* (states 1, 2, and 3) and *Striatocryptus* (states 0, 1, and 3).

52. *Form of glandular duct.* (0) Normal, not saccular; (1) saccular. The typical form of a glandular duct is an elongate sclerotized tube that bifurcates into multiple branches that are suspended in the body cavity (Figs. 50, 53). Among some Cryptophagini, a duct may be saccular and also sclerotized, often with fewer branches (Figs. 51, 74). Based upon microscopic examination of all major lineages of the Cucujoidea, a saccular duct type is probably unique among the Cucujoidea, whereas the elongate bifurcating type is widely distributed in the superfamily. Based on the absence of saccular ducts in the outgroup, I hypothesize that state 0 is plesiomorphic. This character is coded as polymorphic in *Striatocryptus.*

53. *Field of small pores on the hypomeron.* (0) Absent; (1) present. Among some members of the Cryptophagini the surface of the hypomeron has pores that are distributed over most of its surface (Fig. 41). The field of pores may be present only in males of some species. State 1 is absent among the outgroup and it is hypothesized as apomorphic. This character is coded as polymorphic for *Mnioticus.*

54. *Star-like microglandular ducts opening at the base of setal shafts present on the prosternum.* (0) Absent; (1) present. In the cuticle of specimens of Cryptophaginae there are microglandular ducts that radiate away from, or are arranged in a star-like manner around the base of setae in the prosternum of males (Figs. 40, 163). State 0 is present among the outgroup and it is hypothesized as plesiomorphic. This character is coded as polymorphic for *Micrambina* from New Zealand.

55. *Prosternum in front of procoxae.* (0) Short; (1) elongate. In *Hypocoprus*, *Alfieriella*, and *Amydropa* (Figs. 46, 147), the anterior region of the prosternum is more than 2x the length of the prosternal process. In remaining cryptophagids and the outgroup, the length of the anterior portion of the prosternum is equal to or less than that of the prosternal process. State 1 is absent among the outgroup and is hypothesized as apomorphic.

56. *Glandular duct of prosternal process.* (0) Absent; (1) present. A single median glandular duct occurs in the prosternal process among species of Cryptophagini (Fig. 40). This duct is absent in the outgroup and, therefore, state 1 is hypothesized as apomorphic.

57. *Pit on the mesepimeron.* (0) Absent; (1) present. A distinct pit is present at the anterior corner of the mesepimeron among Cryptophaginae (Figs. 73, 139) and some Atomariinae. This pit may contain setae; however, the number of setae and their presence/absence is highly variable. This pit has been referred to as a pocket by Crowson and Sen Gupta (1971). In cryptophagids this structure is a distinct cylindrical pit, however, among some members of the Languriidae it may be more like a cavity or a pocket. A pit is also present in Cavognathidae. Because both states occur in members of the outgroup polarity of this character is uncertain. This character is coded as polymorphic for *Micrambe* and *Picrotus*.

58. *Ringlike cuticle in pits on the body.* (0) Absent; (1) present. The cuticle of the cuticular pits on the body (on the mesepimeron and metasternum) of some species of Cryptophaginae contains ringlike structures (Figs. 74, 92, 139). State 0 is present in the outgroup and it is hypothesized as plesiomorphic.

59. *Fusion of the mesepimeron and mesosternum.* (0) Not fused; (1) fused. The mesepimeron and mesosternum are fused in *Alfieriella* and *Amydropa* (Fig. 150). Fusion of these elements is not found among members of the outgroup, although it occurs among other Cucujoidea (some species of Phloeostichidae and Silvanidae). State 1 is not found among members of the outgroup and, therefore, it is hypothesized as apomorphic.

60. *Parallel lines of the mesosternum.* (0) Absent; (1) present. Parallel lines corresponding to the point of articulation with the prosternal process may be present on the mesosternum (Figs. 65, 66, 74, 152). State 1 is distributed among a variety of Cryptophagidae, but is characteristic of Atomariinae. State 0 is present

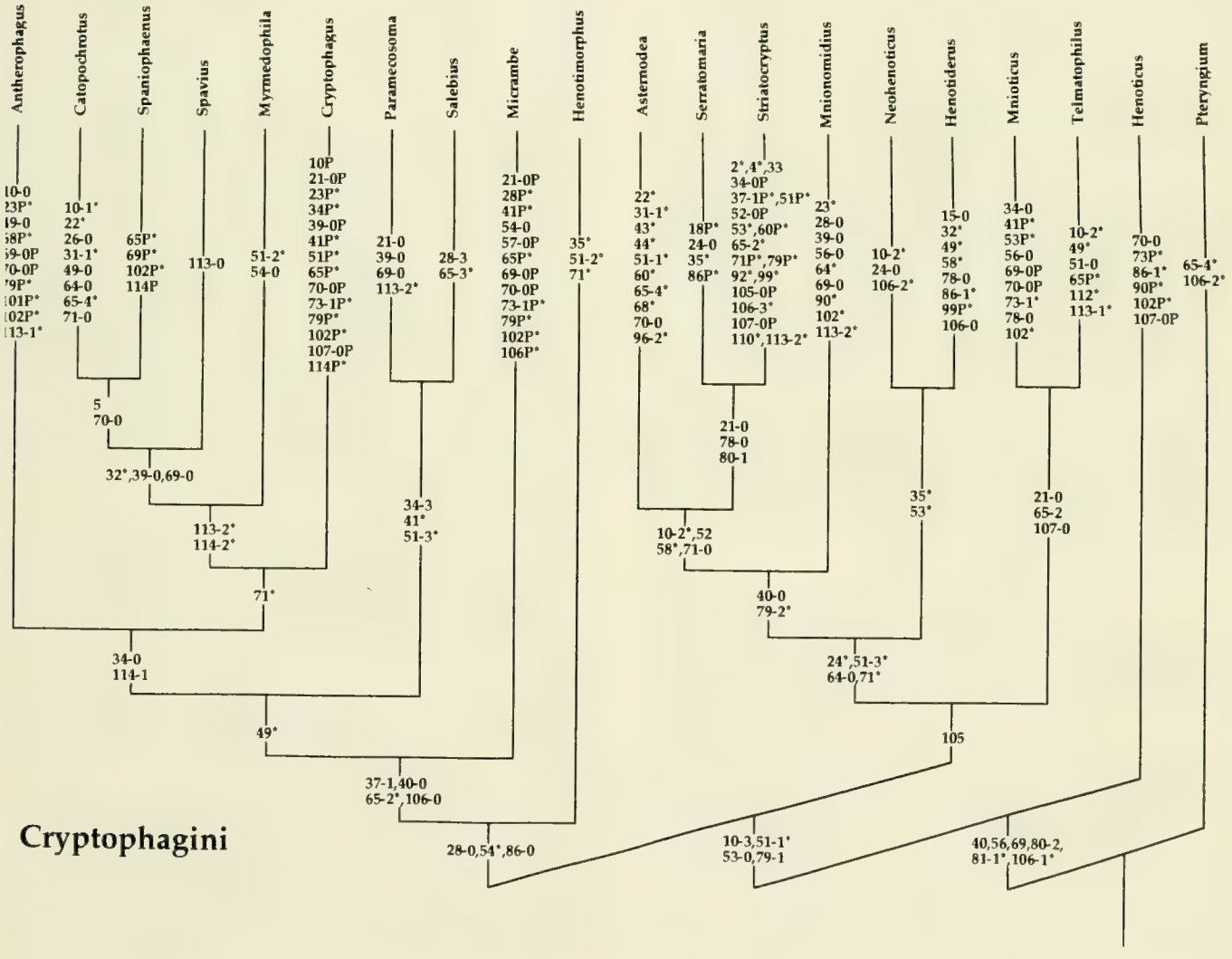


Fig. 3. Cladogram of the genera of the tribe Cryptophagini. (*) = homoplasy, P = polymorphic.

among members of the outgroup, and it is hypothesized as plesiomorphic. This character is coded as polymorphic for *Striatocryptus* and the *A. australis* group.

61. *Mesosternal glandular duct.* (0) Absent; (1) present; (2) present with a callus. A pair of glandular ducts that open onto the surface of the mesosternum is present among some Atomariinae (Figs. 65, 154). These ducts may be associated with a buildup of cuticular material around the pore of the duct (Fig. 152). States 1 and 2 are absent among members of the outgroup and they are hypothesized as apomorphic. This character is coded as polymorphic for the *A. australis* group (states 1 and 2).

62. *Procoxal rests.* (0) present; (1) absent. Procoxal rests on the anterior margin of the mesosternum are characteristic among members of the Cucujoidea and other beetles. However, these are completely absent in *Amydropa* (Fig. 150), *Alfieriella*, and some Atomariinae (Figs. 68, 72). State 0 is present in the outgroup and it is hypothesized as plesiomorphic. This character is coded as polymorphic for *Anitamaria*.

63. *Lateral processes of mesosternal process.* (0) Absent; (1) present. The mesosternal process may have internal lateral processes that fit into the anterior portion of the metasternum between the mesocoxae (Figs. 65, 71, 168). This form of meso-metasternal interlocking mechanism occurs in Atomariinae. State 1 is absent among the outgroup and is hypothesized as apomorphic.

64. *Double knob articulation of the meso- and metasternum.* (0) Absent; (1) present. The internal apex of the metasternum may have two knobs which fit into corresponding recesses of the mesosternum (Fig. 73). Crowson (1980) recognized this feature as a character that unites species of Cryptophaginae, but was unaware that it has a variable distribution within this group. A similar type of meso-metasternal interlocking mechanism occurs in many members of Languriidae, Erotylidae and *Priasilpha* (Phloeostichidae). State 0 is present among the outgroup and, therefore, it is hypothesized as plesiomorphic.

65. *Width of mesosternal process (R = width of mesosternal process) to that of mesocoxa.* (1) $R < 1/3$ (Fig. 67); (2) $2/3 > R < 1$ (Fig. 151); (3) $R = 1$ (Fig. 73); (4) $R > 1$ (Figs. 74, 149). The width of the mesosternal process is variable, and I have contrasted its variation of size in relation to the width of the coxa. Because the variation of this character is consistent among separate groups of terminal taxa it can be gap coded into separate character states. States 1-3 occur in the outgroup, therefore, the polarity of this character is uncertain. This character is coded as polymorphic (states 2 and 3) for *Atomaria, Cryptophagus, Micrambe, Spaniophaenus, Telmatophilus,* and *Caenoscelis.*

66. *Outward closure of the mesocoxal cavity by the metasternum.* (0) Present; (1) absent. The mesocoxal cavity typically comes into contact with the mesepimeron among members of the lower cucujoids; but, among cryptophagids, the mesocoxal cavity is closed laterally by the metasternum (Figs. 73, 74, 149-151). State 0 is present among the outgroup and it is hypothesized as plesiomorphic.

67. *Width of submesocoxal bead.* (0) Narrow; (1) wide. A bead which is present below the mesocoxa on the metasternum may either be narrow (Fig. 73) or relatively wide or thick (Fig. 67). A thick bead is characteristic for some species of Atomariinae. State 0 is present in the outgroup and it is hypothesized as plesiomorphic. This character is coded as polymorphic for *Atomaria* and *Anitamaria.*

68. *Longitudinal metasternal line.* (0) Present; (1) absent. Usually there is a median longitudinal line of variable length present on the metasternum of Cryptophagidae (Fig. 73). State 0 is present in the outgroup and its absence (state 1, Fig. 74) is hypothesized as apomorphic. This character is coded as polymorphic for *Anitamaria, Salltius,* and *Microphagus.*

69. *Metasternal pit below mesocoxa.* (0) Absent; (1) present. State 1 is present in Cryptophagini (Figs. 73, 74). Its size may vary, and if it is small, it may be contained within the submesocoxal bead. Also there may be setae present within the pit (Fig. 92), but the number and presence/absence of these vary considerably among the taxa examined. State 0 is present in the outgroup and it is hypothesized as plesiomorphic. This character is coded as polymorphic for *Antherophagus, Micrambe, Mnioticus,* and *Spaniophaenus.*

70. *Submesocoxal glandular duct.* (0) Absent; (1) present. There are small glandular ducts behind and between the mesocoxal cavities on the metasternum of some species of Cryptophagini (Figs. 73, 74). These may be difficult to locate on the metasternum, but they are separate structures from those that may be associated with setae. State 1 is absent among the outgroup, and, therefore, it is hypothesized as apomorphic. This character is coded as polymorphic for *Antherophagus, Cryptophagus, Micrambe* and *Mnioticus.*

71. *Metasternal glandular duct.* (0) Absent; (1) present. Each side of the disc of the metasternum bears a single glandular duct among many species of Cryptophagini and Atomariinae (Figs. 67, 73, 74, 169). Although the diameter of these ducts varies between members of these taxa (atomariine ducts are larger [about 0.005 mm] than those that are present among the cryptophagines [about 0.003 mm]), the ducts are present in the same position. State 0 is present among the outgroup and is hypothesized as plesiomorphic. This character is coded as polymorphic for *Striatocryptus.*

72. *Concentration of setae at pore of glandular duct.* (0) Absent; (1) present. Among those taxa that bear glandular ducts of the metasternum and ventrites, only some species of the Atomariinae have a dense cluster of setae about the glandular duct pores (Fig. 169). State 0 is present among the outgroup and is hypothesized as plesiomorphic.

73. *Anterior tendons of the metendosternite.* (0) Approximate; (1) widely separate; (2) absent. Among those taxa that are brachypterous, the anterior tendons of the metendosternite become widely separate (many Cryptophaginae, Fig. 85) or are absent completely (*Amydropa,* and *Alfieriella*). Also coupled with this character is a reduction in the relative length of the metasternum; therefore, this latter character is not included in this analysis. State 1 is absent among members of the outgroup and is hypothesized as apomorphic. This character is coded as polymorphic for *Cryptophagus* (states 0 and 1), *Henoticus* (states 0 and 1), and *Micrambe* (states 0, 1, and 2).

74. *Basal plate of the metendosternite.* (0) Transverse; (1) trapezoidal. The base of the metendosternite is composed of a broad plate that is either transverse (Figs. 85, 89) or trapezoidal (Fig. 86). The former condition is widespread among Cryptophagidae, and the latter condition is present among a few species of Atomariinae. State 0 is present among the outgroup and, therefore, is hypothesized as plesiomorphic.

75. *Metepimeron.* (0) Parallel-sided; (1) greatest width in apical half. State 0 occurs in most Cryptophagidae, but, *Amydropa* and *Alfieriella* have state 1 (Fig. 150). State 0 is present among the outgroup and, therefore, it is hypothesized as plesiomorphic. This character is coded as polymorphic for *Amydropa* and *Alfieriella.*

76. *Shape of meta-intercoxal process.* (0) About as long as wide; (1) wider than long. The shape of the meta-intercoxal process is variable in form among lower cucujoids, but in cryptophagids it is usually rounded or slightly square at its apex. Its relative length and width is useful as a character for cryptophagids. A relatively broad intercoxal process occurs in *Picrotus,* some Atomariinae (Fig. 149), and *Hypocoprus.* A relatively broad process is absent among the outgroup, and therefore, state 1 is hypothesized as apomorphic.

77. *Metasubcoxal line.* (0) Absent; (1) present. Metasubcoxal lines, or femoral lines, may be present among a few species of Cryptophaginae and Atomariinae (Figs. 75, 77). Their relative lengths vary, but they are relatively small in Cryptophagidae and not as well developed as they are in other beetle families. State 0 is present among the outgroup and is hypothesized as plesiomorphic.

78. *Length of ventrite 1.* (0) Equal to each of the remaining ventrites; (1) longer than each of the remaining ventrites. State 1 occurs among most Cryptophagidae (as in Fig. 79). This character had been recognized by Sen Gupta and Crowson (1971) as a character distinguishing the family from other taxa presently no longer included in the family. The length of the ventrite is taken at the sides and does not include the length contributed by the intermetacoxal process. State 0 occurs in a few species of Cryptophaginae, *Hypocoprus*, and the outgroup and, therefore, is hypothesized as plesiomorphic.

79. *Glandular ducts on the disk of the ventrite 1.* (0) Absent; (1) present as a single duct; (2) present as two ducts. States 1 and 2 occur in many Cryptophagini; in contrast, only state 2 occurs in Atomariinae (Figs. 75, 77). States 1 and 2 are absent among the outgroup, and they are hypothesized as apomorphic. This character is coded as polymorphic for *Cryptophagus* (states 0 and 1), *Antherophagus* (states 0 and 1), *Micrambe* (states 0 and 1), and *Striatocryptus* (states 1 and 2).

80. *Number of glandular ducts at the lateral edge of each ventrite.* (0) None; (1) one; (2) two. Members of both Atomariinae and Cryptophagini have glandular ducts that flank the lateral margins of the ventrites. However the number of glands varies from one (Atomariinae, Figs. 75, 77) to two (most Cryptophagini, Fig. 76). Also, the relative size of the ducts of Cryptophagini are smaller than those among members of the Atomariinae. States 1 and 2 do not occur in the outgroup, and they are hypothesized as apomorphic.

81. *Distribution of glandular ducts of ventrites.* (0) Absent; (1) present on ventrites 1-4; (2) present on ventrites 1-5; (3) present on visible sternites 2-4. All states are present in Atomariinae, in contrast, only state 1 is present in Cryptophagini. States 1-3 are absent among the outgroup and these are hypothesized as apomorphic.

82. *Shape of ventrite 5.* (0) Evenly arcuate; (1) lobed in the middle. State 1 occurs in some Atomariinae (Figs. 80, 81) where the margin may be sinuate or lobed in the middle. State 0 is present among the outgroup and is hypothesized as plesiomorphic.

83. *Posterior margin of ventrite 5 with crenulations.* (0) Absent; (1) present. State 1 occurs in some Cryptosomatulini (Fig. 82). These crenulations are absent among the outgroup, therefore, state 1 is hypothesized as apomorphic.

84. *Surface of ventrite 5.* (0) Unmodified; (1) with asperities; (2) with thickened setae or pegs. A field of asperities is associated with elongate setae on ventrite 5 among some Atomariinae (Figs. 80, 153). Also in this region there are thick setae or spines among some Caenoscelini (in one species of *Caenoscelis* the male lacks these modified pegs). States 1 and 2 are absent among the outgroup, and they are hypothesized as apomorphic.

85. *Modified spiracle.* (0) Absent; (1) present. The spiracle on abdominal segment 7 is modified with a callus of cuticular material with distinct microsculpture in some Cryptosomatulini (Figs. 84, 170, 173). Similar structures occur in the spiracles of *Priasilpha* (Phloeostichidae) and *Uleiota* (Silvanidae). In one specimen of *Caenoscelis* the spiracle opening is subtended by an elongate chamber and is not modified with cuticular material. Although the shape of the modified spiracle varies from round (most Cryptosomatulini) to elongate (*C. gibbipennis* group) they appear similarly modified. State 1 is absent among the outgroup and it is hypothesized as apomorphic.

86. *Absence of spiracles on abdominal segments.* (0) 1 - 7 present; (1) 7 absent; (2) 6 and 7 absent; (3) 5 - 7 absent; (4) 5 and 6 absent. The number of abdominal spiracles varies among Cryptophagidae. Spiracles present on abdominal segments 1 - 7 are probably present in the cryptophagid groundplan because this is characteristic in many cucujoids, including the members of the outgroup and numerous species in the Cryptophagidae. The number of abdominal spiracles among cryptophagids appears to be attributed to secondary losses. Because these losses are consistent among the taxa, or the segments, they are probably serially homologous and, therefore, treated as the same character. With the exception of state 4 (present in *Amydropa*), losses occur from the posterior to the anterior. States 1-4 are absent among members of the outgroup and they are hypothesized as apomorphic. This character is coded as polymorphic (states 1 and 2) for *Serratomaria* and the *A. australis* group.

87. *Spermathecal duct.* (0) Unsclerotized; (1) sclerotized. The spermathecal duct is typically unsclerotized and attaches to a sclerotized spermatheca. However among some species of atomariines the spermathecal duct is sclerotized and often coiled or convoluted (Figs. 97, 98, 171, 172). State 0 is present among the outgroup and is hypothesized as plesiomorphic. This character is coded as polymorphic for *Atomaria, A. australis* group and unknown in members of *Catopochrotus, Henotimorphus, Mnionomidius, Atomaroides*, and *Cryptafricus.*

88. *Spiculum gastrale of female.* (0) Present; (1) absent. State 1 occurs in some Atomariinae. Because state 1 does not occur in the outgroup, it is, therefore, hypothesized as apomorphic. This character is coded as unknown for *Catopochrotus, Henotimorphus, Mnionomidius, Atomaroides*, and *Cryptafricus.*

89. *Ovipositor.* (0) Well developed; (1) reduced. The ovipositor is reduced to two elongate struts in some Atomariinae. Because of this drastic reduction, it is difficult to determine the homologies among these elements to those structures present in the original ovipositor. A well-developed ovipositor is present in the outgroup, and, therefore, state 1 is hypothesized as apomorphic. This character is coded as unknown for *Catopochrotus, Henotimorphus, Mnionomidius, Atomaroides*, and *Cryptafricus.*

90. *Orientation of the aedeagus in the abdomen.* (0) Vertical; (1) horizontal. Among most Cryptophagini and Caenoscelini the aedeagal orientation is vertical. However, among some atomariines, all cryptosomatulines, and most picrotines, the aedeagal orientation is horizontal. Among the outgroup, the aedeagus is vertical; therefore, state 0 is hypothesized as plesiomorphic. This character is coded as polymorphic for *Anitamaria* and unknown for *Cryptafricus, Serratomaria, Salltius, Tisactia, Alfieriella, Amydropa*, and *Dernostea.*

91. *Apex of the endophallus.* (0) Rounded; (1) notched. The apex of the endophallus may be notched, forming two short lobes among some Atomariinae (Figs. 104, 110). Among the remaining Atomariinae the tip of the endophallus is rounded (as in Fig. 113). State 0 is present among the outgroup and is hypothesized as plesiomorphic. This character is coded as unknown for *Cryptafricus* and *Dernostea.*

92. *Arms of tegmen.* (0) More or less separate or narrowly fused at the distal ends; (1) broadly fused and forming an elongate process. The arms of the tegmen (= basal piece) are typically separate or slightly joined at their tips by a thin membrane among most Cryptophagidae (Figs. 111, 114, 116, 118 and also see Figs. 12-14 in Bousquet 1989). The tips may be solidly fused when the endpiece is arcuate (e.g., some species of Caenoscelini). Among Atomariinae (Figs. 104, 105, 112, 113), *Striatocryptus* (Fig. 117), and *Hypocoprus*, the arms are solidly fused and form an elongate process. State 1 is absent among the outgroup and it is hypothesized as apomorphic. This character is coded as unknown for *Cryptafricus* and *Dernostea.*

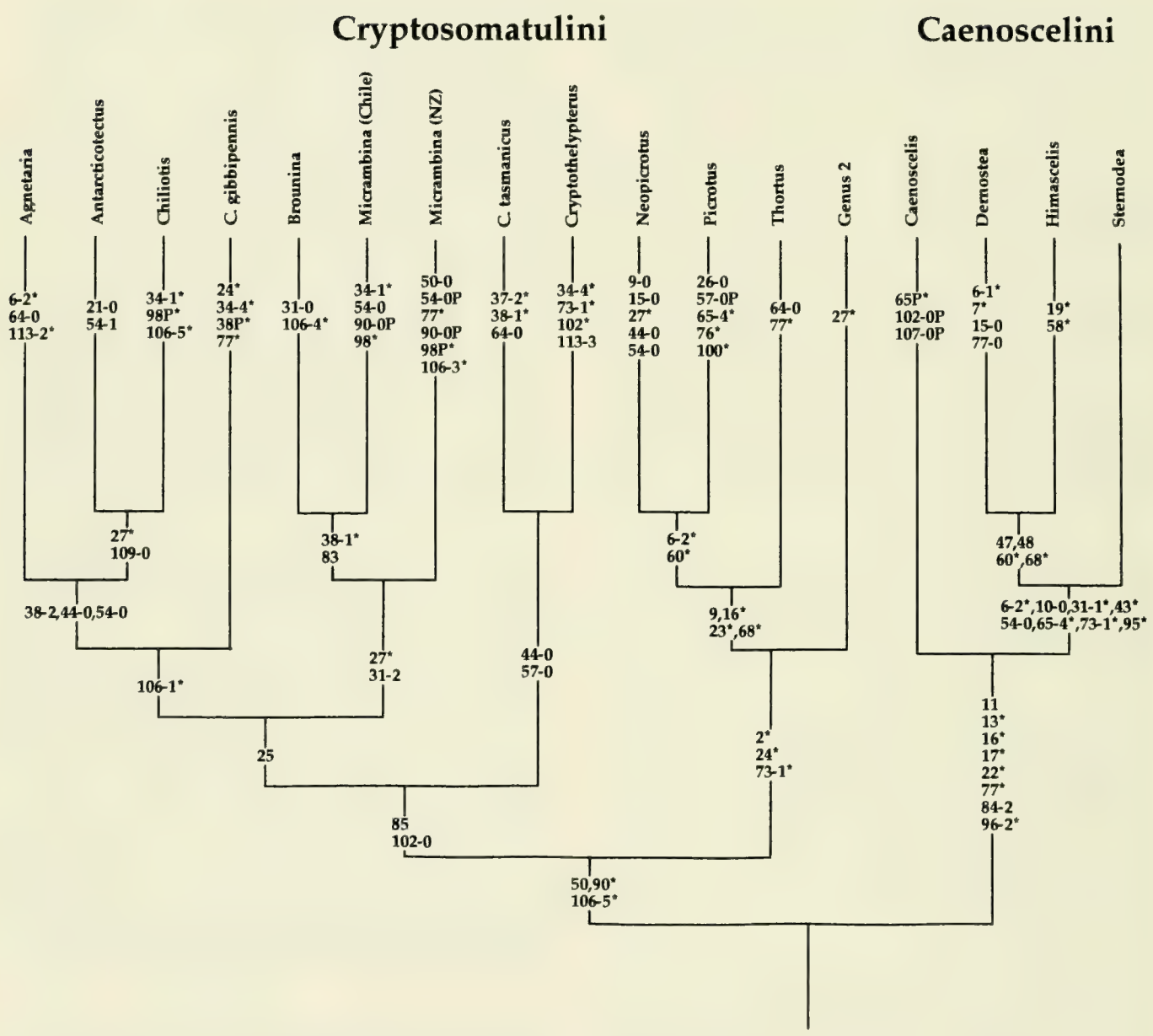


Fig. 4. Cladogram of the genera of the tribes Cryptosomatulini and Caenoscelini. (*) = homoplasy, P = polymorphic.

93. *Articulated parameres.* (0) Present; (1) absent; (2) fused. Among many members of the cucujid-line, the parameres are distinctly separate articulating segments (Figs. 111, 114, 115-117). They become fused into a single lobe in some species of *Caenoscelis,* and in these species there is a distinct line that separates the parameres. In contrast, Atomariinae (Figs. 112-113, 105, 107, 109) and *Hypocoprus* completely lack the articulating parameres and it is uncertain if the apex of the endophallus is actually a result of fusion or loss of the parameres. This type of aedeagus does not occur among members of the outgroup (although it is present in other lower cucujoids) and, therefore, state 1 is hypothesized as apomorphic. This character is coded as unknown for *Cryptafricus* and *Dernostea.*

94. *Spiculum gastrale of male.* (0) Symmetrical; (1) asymmetrical. State 0 occurs in most Cryptophagidae (Figs. 99, 100); however, some Atomariinae have state 1 (Figs. 101, 102). State 0 is present among the outgroup and it is hypothesized as plesiomorphic. This character is coded as polymorphic for *Anitamaria* and unknown for *Himascelis* and *Dernostea.*

95. *Spiculum gastrale of male.* (0) Narrowed; (1) broad. Among the outgroup and most cryptophagids the shape of the spiculum gastrale is transverse at its base with a long narrow strut (Fig. 100). Among most Atomariinae (Fig. 103) and Caenoscelini, the spiculum gastrale is a broad and somewhat triangular sclerite, without a narrow anterior tendon. Among one group of the Atomariinae, the form of the base is more angular and there is an elongate strut, but this strut it is broader than that condition which occurs in members of the Cryptophagini. State 1 is absent among the outgroup and is hypothesized as apomorphic. This character is coded as unknown for *Dernostea.*

96. *Microsculpture of the prescutum.* (0) Variolate; (1) absent; (2) elongate variolate. The microsculpture of the prescutum may either be variolate (Fig. 90) or absent. If variolate, the microsculpture may be elongate and form poorly-defined lines, in which case it is termed "elongate variolate" (Fig. 158). Because state 0 occurs among the outgroup, states 1 and 2 are hypothesized as apomorphic. This character is coded as polymorphic for *Anitamaria* (states 0 and 1).

97. *Setae on the anterior edge of the prescutum.* (0) Absent; (1) present. State 1 occurs in some Atomariinae (Fig. 158). The number of setae vary and may be an important species level characters. State 0 is present among members of the outgroup and is hypothesized as plesiomorphic.

98. *Elytral impressions.* (0) Absent; (1) present. The disc of the elytra of some species of cryptosomatulines has distinct impressions. In some species of the "*C. tasmanicus*" group the space contained within the impressions may be darker in color. State 0 is present in the outgroup and is hypothesized as plesiomorphic. This character is coded as polymorphic for *Micrambina* from New Zealand.

99. *Punctate stria on elytron.* (0) Absent; (1) present. Among most members of the lower Cucujoidea, the elytral punctation is not arranged into distinct punctural stria (referred to as "confused"); however, in some members of Cryptophagini, the punctures form punctate striae. Among most species of *Henotiderus* the striae are two punctures wide while the striae in *Striatocryptus* are one puncture wide. State 1 is absent among the outgroup and is hypothesized as apomorphic. This character is coded as polymorphic for *Henotiderus.*

100. *Subapical gape of elytra.* (0) Present; (1) absent. At the apices of the elytra there is an "apical gape" formed by exposed flanges of each elytron. This character is present among many members of the lower cucujoids but it has been secondarily lost in some wingless forms (Leschen and Lawrence 1991). This character is not always associated with hind wing loss and is treated as a separate character in this analysis. State 1 is present among *Amydropa* (Fig. 137), *Alfieriella,* and *Picrotus.* State 0 is present among the outgroup and is hypothesized as plesiomorphic.

101. *Epipleuron.* (0) Present to level of posterior margin of metasternum (Figs. 138, 149); (1) present beyond level of posterior margin of metasternum. The form of the epipleuron has been used as a key character for distinguishing cryptophagids from other small cucujoid beetles, such as the smaller languriids that were once included in Cryptophagidae. However, determination of the groundplan for this character in the cryptophagids is obscured by its presence in part of the outgroup. This character is coded as polymorphic for *Antherophagus, Tisactia,* and *Anitamaria.*

102. *Hind wing.* (0) Present; (1) reduced or absent. Hind wing loss is common-place among major lineages of beetles and cryptophagids are no exception. Wings are reduced or absent among many species of Cryptophagidae, and the degree of their reduction varies considerably although most taxa examined have the wings reduced to a small flap. Fully developed hind wings are present among the outgroup; therefore, state 1 is hypothesized as apomorphic. This character is coded as polymorphic for *Antherophagus, Cryptophagus, Henoticus, Micrambe, Spaniophaenus, Caenoscelis, Atomaria,* and the *A. australis* group.

103. *Marginal setae of leading edge of hind wing.* (0) Present only to level of RA+ScP vein; (1) extending beyond level of RA+ScP vein. There is a row of setae on the leading edge of the hindwing (Figs. 94-96), above the RA+ScP vein among most Cryptophagidae. These setae arise from the RA+ScP vein and typically coterminate with it. In contrast, these marginal setae extend far beyond the RA+ScP vein among a few members of the Atomariinae. State 1 is absent among the outgroup and it is hypothesized as apomorphic. This character is coded as unknown for *Mnioticus, Mnionomidius, Dernostea, Himascelis, Sternodea, Cryptothelypterus, Neopicrotus, Picrotus,* genus 2, *Thortus, Amydropa,* and *Alfieriella.*

104. *Basal binding patch on hind wing.* (0) Present; (1) poorly-developed or absent. At the base of the hindwing near the wing articulation, there is a well-developed binding patch of microsetae (Figs. 94-96). These are widespread among Cryptophagidae, but they are absent among some Atomariinae and *Hypocoprus.* State 0 is present among the outgroup and it is hypothesized as plesiomorphic. This character is coded as polymorphic for *Atomaria* and unknown for *Mnioticus, Mnionomidius, Dernostea, Himascelis, Sternodea, Cryptothelypterus, Neopicrotus, Picrotus,* genus 2, *Thortus, Amydropa,* and *Alfieriella.*

105. *Hind wing cell.* (0) Absent; (1) present. A distinct cell is formed by the merging of the CuA_2 vein to the CuA_{3+4}+AA_{1+2} vein among a few Cryptophagini (Fig. 94). This cell is not present among members of the outgroup and, therefore, state 1 is hypothesized as apomorphic. This character is coded as polymorphic for *Striatocryptus* and unknown for *Mnioticus, Mnionomidius, Dernostea, Himascelis, Sternodea, Cryptothelypterus, Neopicrotus, Picrotus,* genus 2, *Thortus, Amydropa,* and *Alfieriella.*

106. *Wing veins.* (0) All wing veins present; (1) MP_3 absent; (2) CuA_{3+4} absent; (3) MP_3 and CuA_{3+4} absent; (4) MP_4+CuA_1 and MP_3 absent; (5) MP_4+CuA_1, MP_3, and CuA_{3+4} absent; (6) CuA_{3+4}+AA_{1+2}, MP_4+CuA_1, MP_3, and CuA_{3+4} absent. There is considerable variation in the presence and absence of the wing veins. There are, at most, 7 veins present (Figs. 94, 95), and with a reduction in the number of the wing veins, RA+ScP, MP_{1+2}, and AA_{3+4} are usually present (except in those forms that are brachypterous). The latter vein usually runs along the inner posterior margin of the wing, when the other veins are absent. Each wing vein loss could have been treated as a separate character, however, when proximal veins are absent the distal veins are also absent. This suggests that wing vein losses may not be independent from one another. Therefore, I treat wing vein reduction as a single multistate character. Determination of the groundplan and homology of this character is obscured by the variable number of veins present in the outgroup and reductions or modifications in cryptophagids. Therefore, a more thorough analysis of wing veins is necessary to establish homologies among the families. However, it is possible that the wing with the largest number of veins may represent a groundplan present among many members of the lower cucujoids. This character is coded as unknown for *Mnioticus, Mnionomidius, Dernostea, Himascelis, Sternodea, Cryptothelypterus, Neopicrotus, Picrotus,* genus 2, *Thortus, Amydropa,* and *Alfieriella.*

107. *Tarsal formula.* (0) 555 in both sexes; (1) 554 in male only; (2) 444 in both sexes. The tarsal formula among male members of the lower cucujoids varies and is commonly 554. A 554 male tarsal formula occurs in most Cryptophaginae (Fig. 124), *Hobartius,* and Cucujidae. A 555 male tarsal formula is present among Atomariinae and some species of brachypterous cryptophagines. A 444 tarsal formula is present in *Atomaroides* and *Cryptafricus* (Fig. 123). State 0 is present among the outgroup and it is hypothesized as plesiomorphic. This character is coded as polymorphic (0 and 1) for *Cryptophagus, Henoticus, Striatocryptus,* and *Caenoscelis.*

108. *Tarsomeres of male.* (0) With modified setae; (1) without modified setae. Males of most Coleoptera have tarsal setae that are apically expanded and presumably used to secure females during courtship. Among Cucujoidea these are most commonly present on tarsomeres 1 - 3 of the pro- and mesotarsi (Fig. 157). They are absent in *Microphagus, Cryptogasterus,* and *Amydropa.* State 1 is absent in the outgroup and it is hypothesized as apomorphic.

109. *Shape of tibia.* (0) Parallel-sided; (1) club-shaped. The tibia is typically parallel-sided and slender or gradually increasing in width distally among members of the outgroup and most cryptophagids

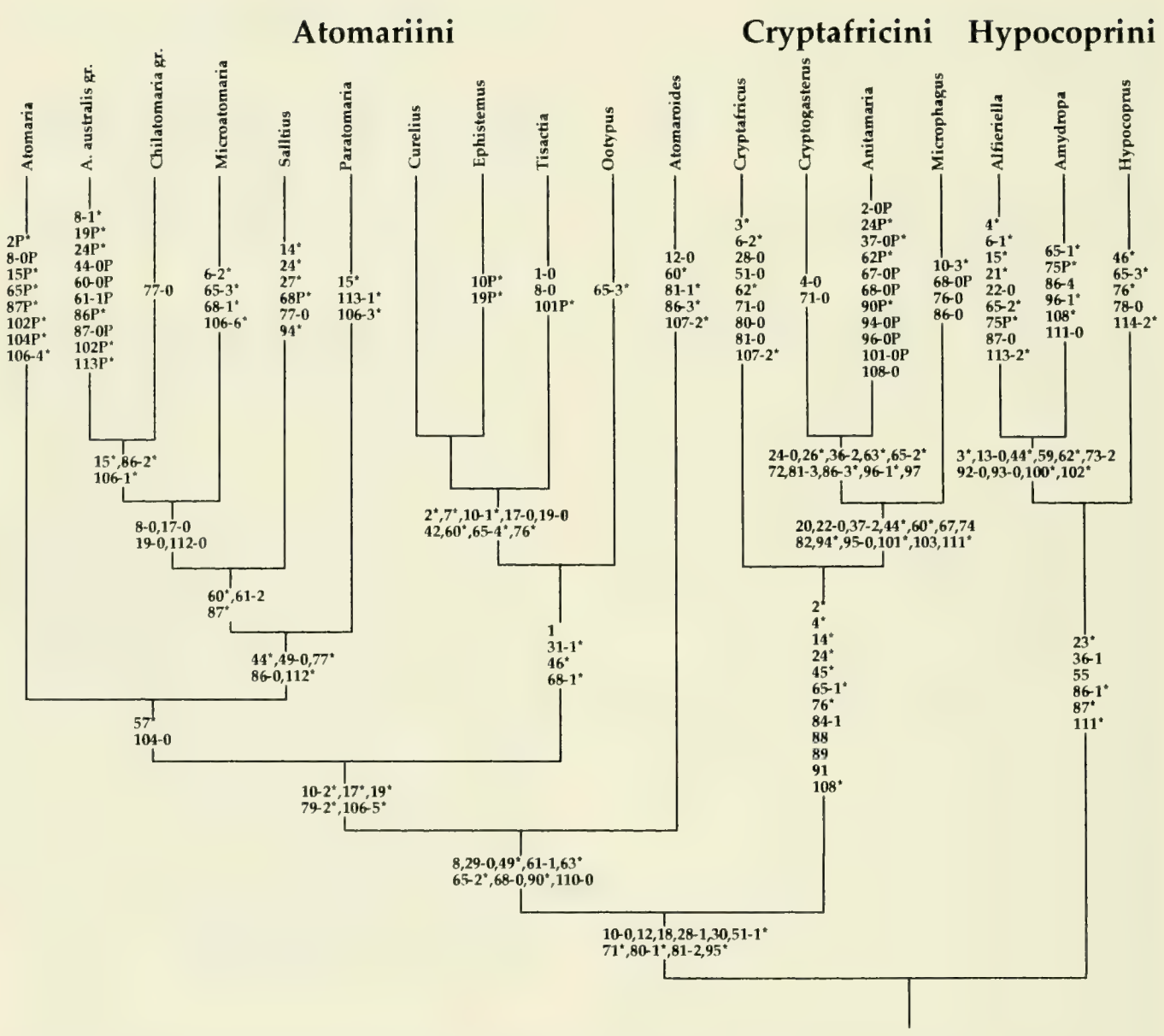


Fig. 5. Cladogram of the genera of the tribes Atomariini, Cryptafricini, and Hypocoprini. (*) = homoplasy, P = polymorphic.

(Figs. 119, 120). In contrast, the tibia is widened in the apical half, the sides are not parallel, and they appear club-shaped among some Cryptosomatulini (Figs. 121, 122), Caenoscelini, and Picrotini. State 1 is absent among members of the outgroup and is, therefore, hypothesized as apomorphic.

110. *Apical fringe of spines of tibia.* (0) Present; (1) absent. The apical fringe of tibial spines which are typically present in beetles (Figs. 119, 121, 122) are absent (Fig. 120) among some Cryptophagidae. State 0 is present in the outgroup and is hypothesized as apomorphic.

111. *Number of tibial spurs.* (0) 2; (1) 1. There are typically two spurs present on the apex of the tibia among most Cryptophagidae (Figs. 119, 121, 122). However, there is only 1 apical spur among some Atomariinae, *Hypocoprus*, and *Alfieriella*. State 0 is present among the outgroup and is, therefore, hypothesized as plesiomorphic.

112. *Tarsomeres.* (0) Slightly or not lobed; (1) distinctly lobed. The tarsomeres may either be filiform (Fig. 155), slightly lobed, or distinctly lobed among Cryptophagidae. It is difficult to distinguish between a filiform and a slightly lobed tarsomere because there is only a slight difference in the length of the tarsal pad. However, a distinctly lobed tarsomere has the tarsal pads well-developed and overlapping below the following tarsomere (Fig. 156). State 1 occurs only in *Telmatophilus* and some Atomariinae. State 0 is present in the outgroup and is hypothesized as apomorphic.

113. *Diet.* (0) Fungus spores and hyphae; (1) pollen; (2) saprophagous; (3) fern spores. Diet can be estimated by examining the contents of the gut (Leschen 1993), and is easily determined by the presence of fungal spores, pollen, and fern spores in the gut. However, a saprophagous diet is assumed by the presence of unidentified material (see Leschen 1993). Among mem-

bers of *Antherophagus*, *Telmatophilus*, and some Atomariinae, the guts are filled with pollen spores. Fern spores are the predominant food of *Cryptothelypterus*. The diet among members of the Cucujidae is fungal spores, while specimens of *Hobartius* have been collected from the fruiting bodies of Basidiomycetes. The exact nature of the diet of Cavognathidae is unknown and larvae have been found on the nestlings of birds (Crowson 1973) or in litter and debris associated with bird nests (Watt 1980); but, gut contents were not examined, and it is possible that cavognathids may be fungal spore feeders. State 0 is present among the outgroup and is hypothesized as plesiomorphic. This character is coded as polymorphic for the *A. australis* group and unknown for *Neohenoticus*, *Brounina*, *Dernostea*, *Himascelis*, *Sternodea*, and *Atomaroides*.

114. *Habitat.* (0) Free living or in bird nests; (1) in bee and wasp nests; (2) in ant nests (3) in termite nests. Most Cryptophagidae are known to be free living and occur in leaf litter, under bark, or anywhere fungal growth is likely to occur. Those species documented with bird nests are not known to be exclusive to this microhabitat. However, there are some species of cryptophagids that are social insect inquilines and occur in the nests of wasps (some species of *Cryptophagus*), bees (*Antherophagus*), ants (*Catopochrotus*, *Myrmedophila*, *Spaniophaenus*, *Spavius*), and termites (*Spaniophaenus*). Members of the outgroup are also free living (although Cavognathidae are present in birds nests [Crowson 1966, 1973]) and do not occur with social insects. States 1-3 are absent among members of the outgroup and, therefore, are hypothesized as apomorphic. This character is coded as polymorphic for *Cryptophagus* (states 0 and 1) and *Spaniophaenus* (states 0, 2, and 3) and unknown for *Neohenoticus*, *Brounina*, and *Dernostea*.

Results: Cladistic analysis, assigning equal weights to all characters (EWC), resulted in over 500 equally parsimonious trees with the following tree statistics: tree length (TL) = 407, consistency index (CI) = 0.366, retention index (RI) = 0.740. Only 500 trees were retained due to computer limitations. A strict consensus tree of these 500 trees is given in Fig. 1. A subsequent analysis using successive approximations character weighting (SAW) resulted in nine trees by two iterations (Fig. 2). These trees are internally consistent and differ in that the relationships among *Ephistemus*, *Tisactia*, and *Curelius*, and a group of several cryptophagines is unresolved (shown as trichotomies in the strict consensus tree). One of these trees was selected arbitrarily and is shown in Figs. 3-5 (character distributions are optimized onto this phylogeny). The SAW trees differ from those EWC trees by the consistent placement of Caenoscelini + Cryptosomatulini, resolution of a major polytomy in and phylogenetic placement of certain genera of Cryptophagini and Cryptosomatulini, and resolution of two polytomies in Atomariini.

Genus 1 is not shown in the cladograms, and is not described in this paper because it is represented in the data matrix by mostly unknown characters and permission to dissect the specimen was not granted. Many internal morphological characters support major branches in the resultant phylogenies, and because these were coded as unknown in genus 1, it was consistently placed at the base of the trees and not grouped with any major lineage.

As previously discussed in the Character Analysis, the polarization for many characters was equivocal due to variation of character states and the uncertainty of relationships among the outgroup confounding character state groundplans. Characters with ambiguous polarities include numbers 2, 4, 10, 14, 15, 18, 20, 21, 22, 26, 27, 46, 57, 65, 92, 95, 101, 106, and 107. In view of the parsimony analysis and the resultant trees, polarity assignment for character numbers 2, 4, 10, 14, 18, 20, 27, 95, 101, and 106 can be inferred by tree structure. Polarity assignments remain equivocal for characters 15, 21, 22, 26, 46, 57, 65, 92, and 107 and must await further study. Characters 33, 66 and 75 are uninformative.

MAJOR LINEAGES AND TAXONOMIC CONCLUSIONS

Although most characters that show support for major lineages as synapomorphies are subject to reversal and homoplasy, I believe that these are *prima facie* evidence for phylogenetic pattern and should not be characterized as "weak". These synapomorphies were discovered based upon a parsimony analysis that included all potential homologies: they are equally informative, whether they are unique and unreversed (which is obviously rare) or convergent.

Crowson (1980) recognized four major lineages within Cryptophagidae: Cryptophaginae (Cryptophagini, Cryptosomatulini, Caenoscelini, Picrotini), Atomariinae, Alfieriellinae, and Hypocoprinae. Based on cladistic analyses, Cryptophaginae form a monophyletic group (Fig. 2, node A) that is sister taxon to Atomariinae + Alfieriellinae + Hypocoprinae (Figs. 1,2, node B) and Atomariinae + Cryptafricini (Fig. 2, node C) + Alfieriellinae + Hypocoprinae (Fig. 2, node D) together form what I refer to as the "atomariine-group" in the following discussion.

EWC cladistic analysis produced some trees in which Caenoscelini + Cryptosomatulini are sister taxon to the Cryptophagini, or the Caenoscelini are sister taxon to Cryptosomatulini + Cryptophagini (Fig. 6, node A). In contrast, SAW produced trees in which Caenoscelini are consistently placed with Cryptosomatulini as sister taxa. Inspection of the 500 trees resulting from the initial EWC analysis revealed that Caenoscelini + Cryptosomatulini occur in about 16% of these trees. Placement of Caenoscelini at a basal position in the SAW trees results in trees that are five steps longer (based on weighted characters).

EWC cladistic analysis produced trees with three different topologies of the following major lineages: Cryptafricini + (Hypocoprini + Alfieriellinae), Cryptafricini + Atomariinae, or Hypocoprini + (Cryptafricini + Atomariinae). These patterns are shown as one polytomy in Fig 1, node B. SAW analysis produced trees in which the relationship Cryptafricini + Atomariini (Fig. 2, node C) is consistent. Inspection of the 500 trees from the EWC analysis showed that Cryptafricini + (Hypocoprini + Alfieriellinae) occurs in 248 trees, Cryptafricini + Atomariinae occurs in 244 trees, and Hypocoprini + (Cryptafricini + Atomariinae) occurs in eight trees. Placement of Hypocoprini + (Cryptafricini + Atomariinae) or Cryptafricini + (Hypocoprini + Alfieriellinae) in the SAW trees results in trees that are 10 steps longer.

Deciding on a set of cladograms on which a classification is to be based can be done by accepting those reconstructions produced by SAW analysis (Carpenter 1988). However, I choose to consider alternative reconstructions present among the original EWC trees. Some of the alternative hy-

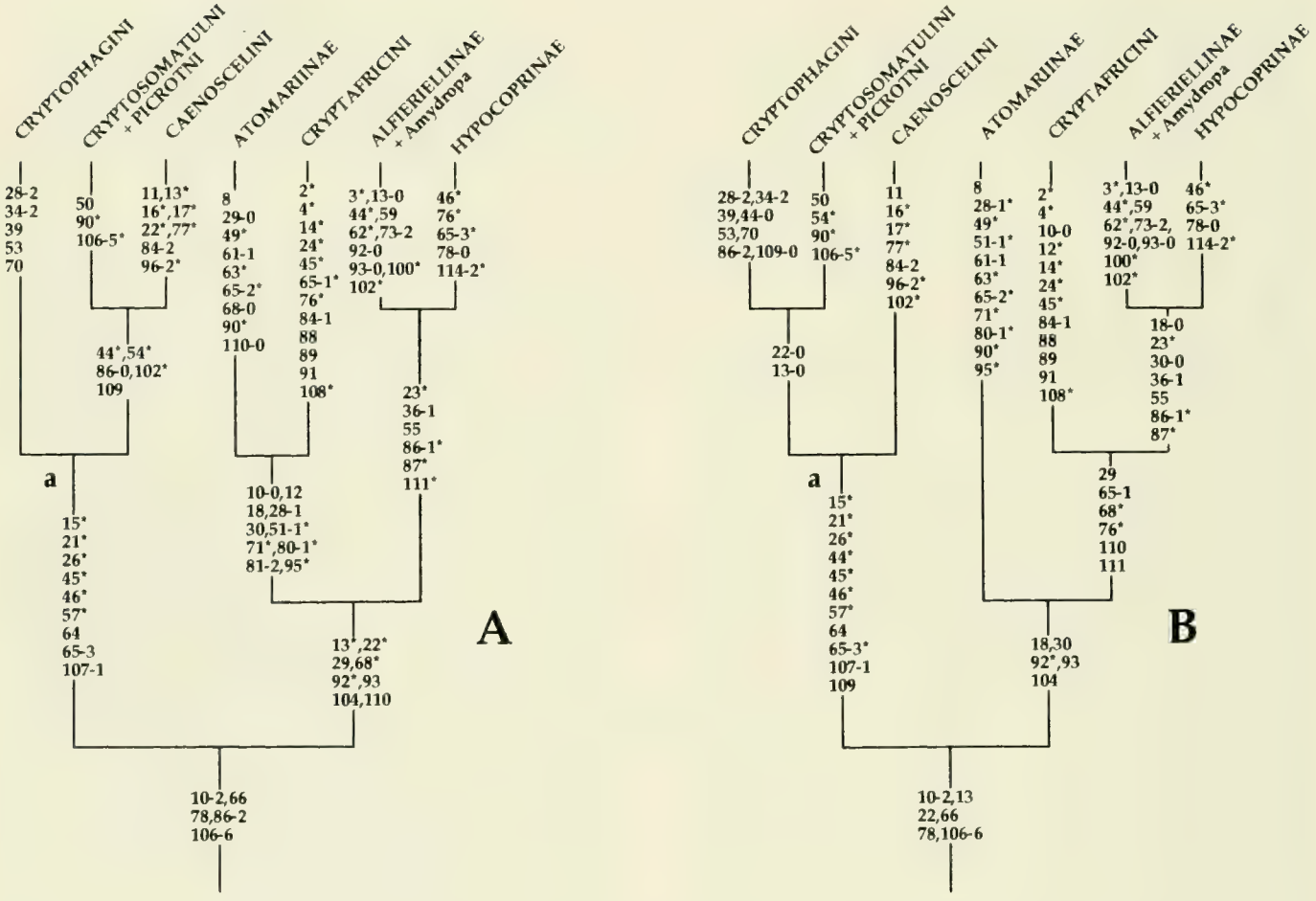


Fig. 6. Alternative phylogenies of higher taxa of Cryptophagidae. A. A phylogenetic reconstruction that shows Cryptosomatulini with Caenoscelini as sister taxa (CON 1). B. A phylogenetic reconstruction that shows Cryptophagini with Cryptosomatulini as sister taxa (CON 2).

potheses discussed above are shown in Fig. 6 and characters are optimized onto these trees. I will refer to these two topologies as condition 1 (CON1), in which Caenoscelini are sister taxon to Cryptosomatulini and Cryptafricini are sister taxon to Atomariinae (showing the distribution of taxa produced by SAW analysis), and condition 2 (CON2), in which Cryptosomatulini is sister taxon to Cryptophagini, and Cryptafricini is sister taxon to Hypocoprini + Alfieriellinae (showing an alternative distribution of taxa produced by EWC analysis). I will refer to the topology Hypocoprini + (Cryptafricini + Atomariinae) as condition 3 (CON 3, not shown). For the purposes of the following discussion, characters are listed first followed by their character number and state (only if the character state is a reversal or part of a multistate character).

Support for the monophyly of Cryptophaginae by unambiguous characters (i.e., those characters that do not vary in their optimization) is based on the internal closure of the procoxal cavity (45) and presence of a double knob at the mesometasternal junction (64). The double knob articulation was suggested as a synapomorphy by Crowson (1980). Seven other characters are concordant with these: presence of a transverse line or ridge on the mentum (15), presence of subgenal spines (21), presence of a transverse line on the vertex of the head (26), external closure of procoxal cavity (46), presence of a mesepimeral pit (57), mesosternal process equal in width to mesocoxa (65-3), and tarsal formula 554 in male (107-1). A 554 tarsal formula in the male was first recognized as a character by Casey (1900). Under CON2 absence of a notch on the hypomeron (44) and a club-shaped tibia (109) provide additional support for the monophyly of Cryptophaginae.

Unambiguous synapomorphies that support Caenoscelini + Cryptosomatulini (CON1) include the absence of a notch on the hypomeron (44) and a club-shaped tibia (109). The following characters are concordant with these: presence of star-shaped microglandular ducts on the prosternum (54), spiracles present on abdominal segments 1 - 7 (86-0), and hind wing absent or reduced (102). An implication of character (102) occurring at this node is that the hind wing would have to be regained in some winged members of *Caenoscelis* and Cryptosomatulini (see below).

Under CON2, the width of the basal labial palpomere (subequal to the terminal palpomere 13-0) and presence of gular sutures (22-0) support the monophyly of the Cryptosomatulini + Cryptophagini. The latter character supports this group unambiguously. Since lineages are supported by the number of characters supporting a particular branch, there is more evidence supporting the hypothesis Caenoscelini + Cryptosomatulini (based on five characters) than the hypothesis Cryptosomatulini + Cryptophagini (based on two characters).

The monophyly of the atomariine group is supported by one or two unambiguous apomorphies. Under CON1, the atomariine group is supported by one unambiguous character (absence or reduction of the basal binding patch of wing, 104) and the following characters which are concordant with this one: basal labial palpomere wider than the terminal one (13), absence of gular sutures (22), presence of a straplike tentorium (29), absence of a longitudinal line on metasternum (68), arms of tegmen broadly fused into an elongate process (92), articulated parameres absent (93), and the absence of an apical fringe of spines on tibia (110). Under CON2, the atomariine group is supported by two unambiguous characters (93 and 104) and the following characters which are concordant with these: 18 (frontoclypeal suture present), 30, and 92.

Unambiguous synapomorphies that support Cryptafricini + Atomariinae (CON1) are the presence of a frontoclypeal suture (18) and anterior arms of the tentorium fused (30). Concordant with these are: absence of dorsal mandibular tubercles (10-0), presence of sensory pores on the surface of the mandible (12), presence of cephalic glandular ducts between the antennal insertions (28-1), presence of one lateral pronotal glandular duct (51-1), presence of a metasternal glandular duct (71), presence of 1 glandular duct on each ventrite (80-1) that are present on ventrites 1- 4 (81-2), and spiculum gastrale of male broad (95).

Unambiguous synapomorphies that support Cryptafricini + (Alfieriellinae + Hypocoprini) under CON2 are: presence of a straplike tentorium (29), absence of a longitudinal line on the metasternum (68), and the absence of an apical fringe of spines on the tibia (110). Concordant with these are: width of mesosternal process less than 1/3 that of mesocoxa (65-1), meta-intercoxal process wider than long (76), and presence of a single tibial spur (111).

Three unambiguous synapomorphies that support the monophyly of the Alfieriellinae + Hypocoprinae are as follows under CON1: eyes reduced to a few facets (23), absence of a lateral pronotal bead (36-1), and prosternum elongate in front of procoxae (55). Concordant with these are: absence of spiracles from abdominal segment 7 (86-1), presence of a sclerotized spermathecal duct (87), and presence of a single tibial spur (111). Four unambiguous synapomorphies that support Alfieriellinae + Hypocoprinae are as follows under CON2: 23, 36-1, 55, and 86-1. Concordant with these are the absence of a frontoclypeal suture (18-0), anterior arms of tentorium separate (30-0), and 87.

Three unambiguous synapomorphies that support the monophyly of Hypocoprinae + (Cryptafricini + Atomariinae) under CON 3 (not illustrated) are as follows: basal labial palpomere wider than the terminal one (13), arms of tegmen broadly fused into an elongate process (92), and articulated parameres absent (93). Concordant with these characters are hypomeron without a notch (44-0) and meta-intercoxal process broad (76). There is more evidence for the relationship Hypocoprinae + Alfieriellinae which is based on six or seven characters listed above.

Since the Linnaean hierarchy functions as an information storage-retrieval system, it can reflect important information gained from cladistic analyses (see recent reviews by de Queiroz and Gauthier 1990, 1992). Based on the branching structure of the cladograms discussed above, I am recognizing three tribes within the Cryptophaginae: Caenoscelini, Cryptosomatulini (including Picrotini, see below), and Cryptophagini. Because the phylogenetic placement of Caenoscelini is problematic (based on the EWC trees), I believe that its categorical rank is best retained as a tribe. Relationships among the atomariine group are also inconsistent, and I recognize this lineage as Atomariinae composed of three tribes: Atomariini (formerly Atomariinae and including Ephistemini and Saltiini, see below), Cryptafricini, and Hypocoprini (including Alfieriellinae, see below).

The inclusion of Alfieriellinae + Hypocoprinae as members of the atomariine group, and for that matter, within the Cryptophagidae (see previous section), is somewhat unsettling. Therefore the monophyly of Cryptophagidae (i.e., the inclusion of Alfieriellinae and Hypocoprinae within the family) must be re-evaluated under a more comprehensive phylogenetic study of Cucujoidea.

Cryptophagini: The monophyly of Cryptophagini is based on the following unambiguous synapomorphies (CON1 and CON2): presence of cephalic glandular ducts on the outside margin of the antennal insertions (28-2), a serrate margin on the pronotum (34-2), and presence of basal pronotal pits (39). Concordant with these under CON1 are the presence of a field of glandular pores on the hypomeron (53) and presence of a submesocoxal glandular duct (70) while under CON2 are the hypomeron with a notch above the procoxal cavity (44-0), 53, 70, abdominal spiracles absent from segments 6 and 7 (86-2) and tibia more or less parallel-sided (109-0).

The phylogenetic patterns within Cryptophagini shown among the cladistic analyses are variable. Consistencies among the EWC trees show three monophyletic groups: *Antherophagus, Salebius* + *Paramecosoma, Cryptophagus* (*Myrmedophila* (*Spavius* (*Spaniophaenus* + *Catopochrotus*))); *Asternodea* (*Serratomaria* + *Striatocryptus*), and *Henotiderus* + *Neohenoticus.* Among SAW trees (Fig. 2), *Micrambe* and *Henotimorphus* are added to the first group (referred to as the *Cryptophagus*-group) and the trichotomy is still present. Synapomorphies for the *Cryptophagus*-group are: absence of cephalic glandular ducts (28-0), presence of star-like glandular ducts on the prosternum (54) and presence of spiracles on abdominal segments 1 - 7 (86-0). The presence of a pronotal angularity (37-1) characterizes many members of this

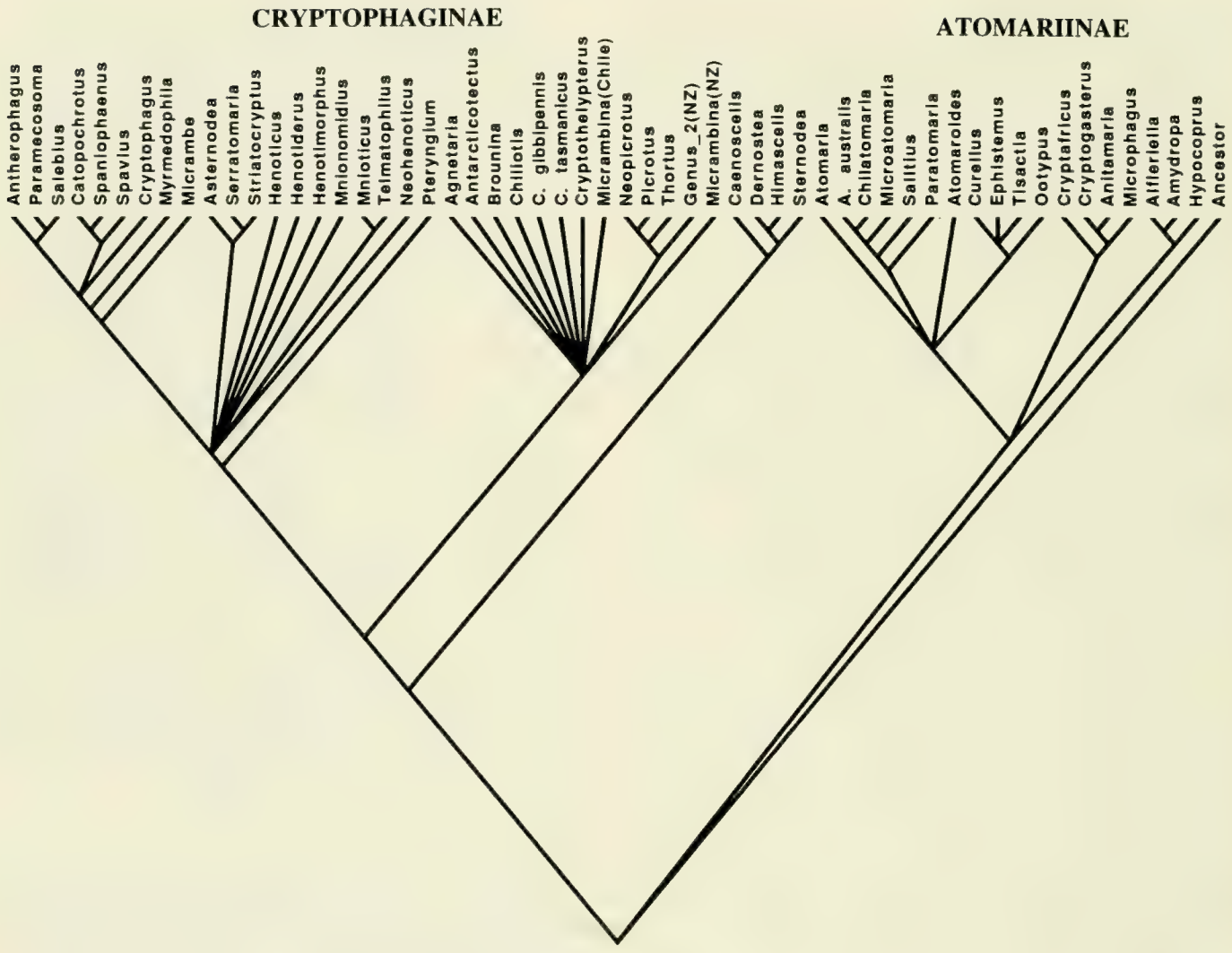


Fig. 7. Strict consensus tree (of 500 trees) of the phylogenetic relationships among members of Cryptophagidae with all characters of equal weight and behavioral characters (113 and 114) removed.

group. The inquiline members of Cryptophagini also occur more or less together in this lineage. The resolution of the relationships among this group may be suspect because *Cryptophagus* may represent a grade of species which are very variable and the genus cannot be defined by a single synapomorphy (see below).

The relationship of *Asternodea* (*Serratomaria* + *Striatocryptus*) is well supported. These taxa are united by several characters (10-2, 52, 58, 71-0), including the presence of bladder-like gland ducts (52), a unique character among Cucujoidea that has been secondarily lost in some species of *Striatocryptus*.

Telmatophilus, which has often been excluded from the Cryptophaginae altogether (e.g., Bousquet 1989), is certainly a member of this tribe based on several characters, including the presence of a wing cell (105) that is unique among members of Cryptophagidae.

Resolution of the relationships among cryptophagine lineages is complicated by character conflicts (shown as a polytomy in Fig. 1) and problematic limits of particular genera. *Cryptophagus* and *Micrambe* are composed of numerous species that are very variable in form and include many flightless species: For example, some species of *Cryptophagus* occurring on islands (*C. ellipticus* and other species on the Canary Islands) and some species of *Micrambe* in montane east Africa have reduced lateral teeth and well-developed angularities on the pronotum. In addition, there is an undescribed flightless species of "*Cryptophagus*" from Oaxaca, Mexico that has three lateral pronotal glandular ducts (most species of *Cryptophagus* have two lateral glandular ducts) associated with an angularity and two prominent lateral teeth (most species of *Cryptophagus* have one prominent lateral tooth). Lastly, there is a group of east Asian *Cryptophagus* (*C. micramboides* and some undescribed species) that have a pronotal margin similar to *Micrambe*; however, these have an anterior glandular duct morphology typical of *Cryp-*

tophagus. There has been confusion on the taxonomic limits of *Cryptophagus* and *Micrambe*; and, for example, these have been treated as the same genus by Bruce (1936). However, based on cladistic analysis, there are characters demonstrating that these genera are separate taxonomic entities (see Figs. 2 and 3). Another existing problem is that *Cryptophagus* may represent a grade of species and, as stated before, it is not defined by a single synapomorphy. Moreover, examination of species-group relationships among *Cryptophagus* may affect the way in which other genera in this group are recognized.

There are two broad informal groups of taxa that I recognize in Cryptophagini. The lineage (Fig. 2) containing *Henotimorphus, Micrambe* and others are shown to be monophyletic based on three characters (28-0, 54, and 86-0) and contain most of the taxa that have a pronotal angularity: I have referred to this lineage as the *Cryptophagus*-group. Another group of taxa that typically do not have a pronotal angularity but usually have well defined serrations on the lateral margin of the pronotum is not monophyletic but represents a grade. This more basal group of taxa I refer to as the *Henoticus*-group.

Internal support for many groupings consists of one or two synapomorphies. The relationships among cryptophagine genera are tenuous, and future cladistic analyses should include a detailed study of the species of *Cryptophagus* and additional characters from other data sets.

Cryptosomatulini: Support for the monophyly of Cryptosomatulini is shown only in the SAW analyses. However, when characters are eliminated from the original data matrix (see next sections), the tribe is demonstrably monophyletic.

Crowson (1980) recognized the tribes Cryptosomatulini and Picrotini as separate taxa among Cryptophaginae, and that Picrotini and Caenoscelini to be sister taxa. Crowson based his interpretation of sister relationship of Caenoscelini and Picrotini upon two larval characters (presence of heavily sculptured cuticular surface and similarities of the urogomphi; note that larvae were not reared) and three adult characters (2-segmented antennal club, antennal insertions approximate, and a broad mesosternal process). Although Picrotini and Cryptosomatulini are placed phylogenetically close on the trees, the adult characters used by Crowson either do not fall at the appropriate positions on the tree, or are not well formulated as characters (e.g., if the antennal insertions are approximate this can be associated with a frontal boss, as in members of Caenoscelini, or a narrow carina as in some members of *Thortus*) and can be misinterpreted as homology. Regarding larval characters, larvae with heavily sculptured surfaces have been collected in association with adults of Cryptosomatulini (New Zealand *Micrambina*) and larvae with strongly developed asperities occur among some Cryptophagini (*Henoticus* and *Henotiderus*). I can't comment on the significance of urogomphal structure as a character linking Caenoscelini and Picrotini because definitive (reared) larvae of these tribes are not known.

The monophyly of Picrotini determined by Crowson (1980) was based on character states present among adults and associated larvae among members of *Picrotus* and *Thortus* (absence of larval ocelli and adult hind wings). Indeed the tribe "Picrotini", if genus 2 and *Neopicrotus* are included, appear monophyletic based on 3 characters (2, 24, 73-1), and, depending on the choice of character optimization, hind wing reduction (102) supports this grouping (see below). The absence of larval ocelli may be widespread in Cryptophagidae, because first instar larvae of some Cryptophagini (*Antherophagus* and *Cryptophagus*) do not have these structures. What is more important, however, among the original 500 trees based on EWC analysis, Cryptosomatulini and Picrotini may be paraphyletic; *Cryptothelypterus* (also wingless) and other taxa are often grouped with members of Picrotini. Therefore, I synonymize the Picrotini and Cryptosomatulini. This does not preclude the recognition of Picrotini as a subtribe if future cladistic studies yield distinct monophyletic groups among Cryptosomatulini. Cryptosomatulini is defined by the following synapomorphies (CON1): presence of microtubules in the body (50), aedeagus orientation horizontal (90), and wing veins MP_4+CuA_1, MP_3, and CuA_{3+4} absent (106-5). Characters 50 and 90 are unambiguous. Also note that character 106-5 has been mapped onto the basal portion of the cryptosomatuline phylogeny by PAUP because some of the basal taxa were coded as unknown in the data matrix. The monophyly of Cryptosomatulini under CON2 is based on three unambiguous synapomorphies: presence of star-shaped glandular ducts on the prosternum (54), 50, and 90. Character 106-5 is concordant with these.

Although relationships among members of Cryptosomatulini are provisional, there are some interesting implications for the monophyly of certain groups. For example, the majority of apterous forms group together (exclusive of *Cryptothelypterus*) and the genus *Micrambina* may be paraphyletic. *Micrambina* includes taxa from South America and New Zealand, and these occur separately on the cladogram (Crowson has labeled museum specimens of New Zealand *Micrambina* as *Paramicrambina*). Any changes in the generic limits of the tribal members of Cryptosomatulini based on this analysis would be hasty because the relationships shown are based on exemplar taxa, and additional "genus-level" taxa available for treatment in a future cladistic analysis should result in different phylogenetic patterns. Moreover, some characters excluded from the data matrix because they were autapomorphies in this analysis may be synapomorphies shared with taxa not used in this study. Therefore, a thorough cladistic analysis of the tribe Cryptosomatulini is necessary to test the phylogenetic relationships and monophyly of currently recognized genera, place undescribed forms into appropriate genera, and remove taxa currently in *Cryptophagus* to other genera or provide them with new names.

Caenoscelini: Support for the monophyly of Caenoscelini is based on the following unambiguous apomorphies under CON1: incisor lobe of left mandible with serrations (11; unique and unreversed), width of basal palpomere larger

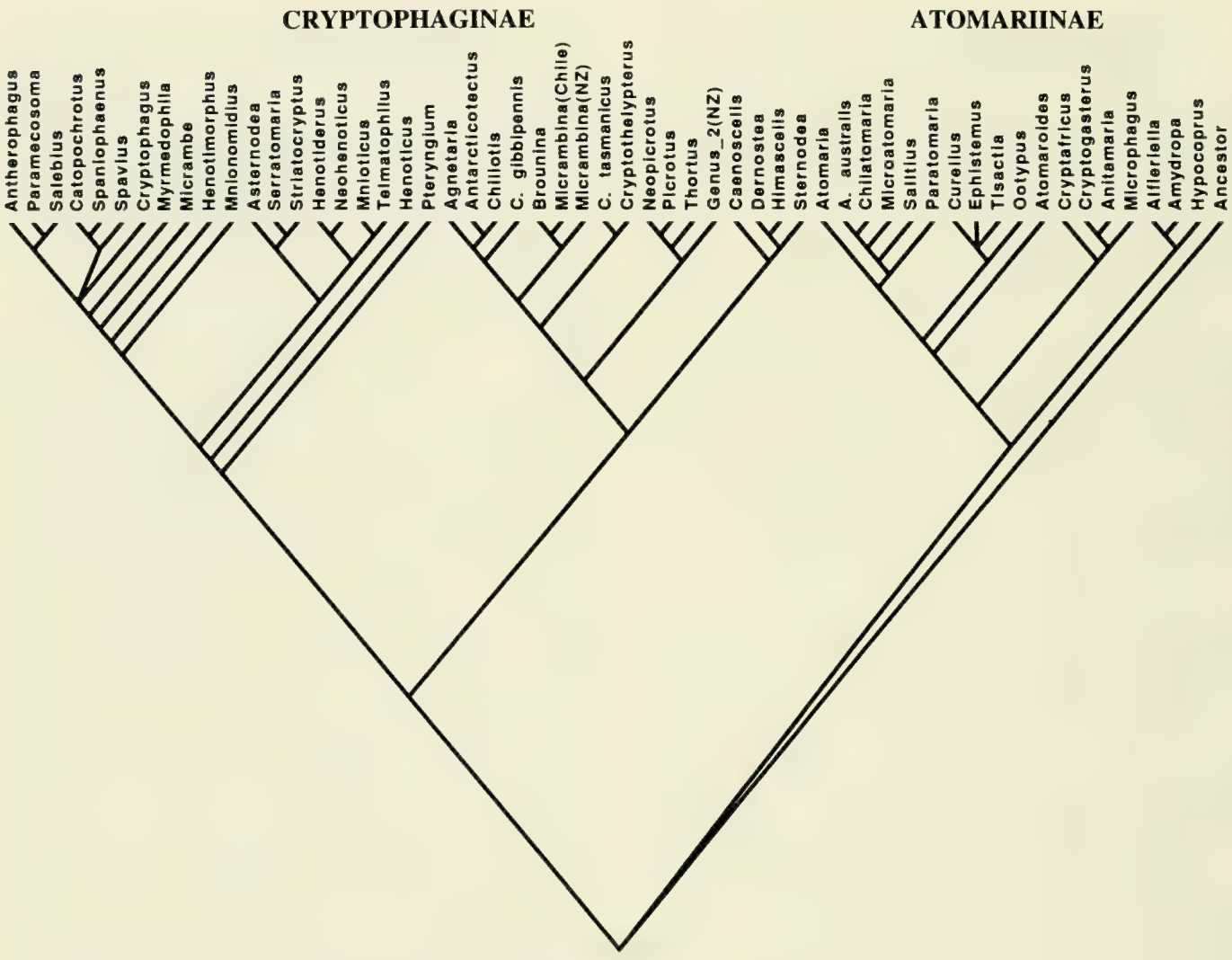


Fig. 8. Strict consensus tree (of nine trees) of the phylogenetic relationships among members of Cryptophagidae with successive approximations weighting of characters with behavioral characters (113 and 114) removed.

than that of terminal palpomere (13), presence of a ridge surrounding the antennal concavity (16), presence of a boss on the front of the head (17), presence of metasubcoxal lines (77), presence of thickened setae or pegs on the ventrite 5 (84-2; unique and unreversed), and the microsculpture of the prescutum elongate variolate (96-2). An additional character concordant with these is the absence of gular sutures (22). Under CON2 the following characters are unambiguous synapomorphies: 11, 16, 17, 77, 84-2, and 96-2. Concordant with these are: 22 and the absence of a hind wing (102). The relationships among members of Caenoscelini are well resolved. *Caenoscelis* is sister taxon to the remaining flightless members that form a monophyletic group based upon several characters (see Fig. 4). Recognition of the two tribes proposed by Casey (1900), Sternodeini and Caenoscelini, is unnecessary because the number of genera taxa contained within them is small.

Hypocoprini: Crowson (1980) placed *Alfieriella* in its own subfamily, Alfieriellinae, and postulated that *Amydropa* should belong within it. Hypocoprinae, which has been included in a variety of families (Cryptophagidae, Hypocoridae, Monotomidae, Cucujidae), is sister taxon to the Alfieriellinae. Consistent with the branching arrangement of the phylogeny, I place Alfieriellinae within Hypocoprinae, and change the rank of the latter to tribe. Besides, the name Alfieriellinae is currently unavailable (Pakaluk et al. 1995). The characters that define Hypocoprini were mentioned previously.

Atomariini: The tribe Atomariini (formerly subfamily) was previously defined by the presence of glandular ducts on the thoracic and abdominal sternites, aedeagus lacking articulated parameres, and larvae with bicameral spiracles (Crowson 1980). Crowson (personal communication) also

included undescribed forms that I have placed in Cryptafricini (see below), and clearly his concept of Atomariini is paraphyletic with respect to the phylogenetic placement of Cryptafricini. Unambiguous synapomorphies that support the monophyly of Atomariini include the following (CON1): funicle shape conical (8), two glandular ducts present in the anterior portion of prosternum (49), presence of mesosternal glandular duct (61-1), lateral processes present on the margins of the mesosternal process (63), presence of a longitudinal line on metasternum (68-0), and orientation of aedeagus in body horizontal (90). Concordant with these are: shape of posterior portion of tentorium in the form of a straight transverse bar (29-0), width of mesosternal process 2/3 that of mesocoxa (65-2), and tibia with apical fringe of spines (110-0). Under CON2 the following are unambiguous synapomorphies for Atomariini: 8, presence of cephalic gland ducts (28-1), 49, presence of a single lateral pronotal glandular duct (51-1), 61-1, 63, presence of metasternal glandular duct (71), ventrites with one glandular duct on each side (80-1), 90, and spiculum gastrale of male broad (95). Concordant with these is character 65-2.

Casey (1900) included *Curelius* and *Ephistemus* in Ephistemini, a group composed of species that are convex and oval, and concluded that these were related to Atomariini through similarities with *Tisactia* that he placed in Atomariini. Based on my analysis, *Tisactia* should be included in Ephistemini, if it were to be recognized as a valid taxon. These form a distinct monophyletic lineage represented as a hard polytomy in strict consensus trees within Atomariini (Figs. 1,2, and 5). Retaining Ephistemini as a tribe would create a paraphyletic grouping of the remaining members of Atomariini.

Salltiini was erected by Crowson (1980) for the single genus *Salltius,* which was noted as a member of a group of genera containing undescribed south temperate forms. The tribe Atomariini is paraphyletic with respect to the placement of Salltiini. Consistent with the branching sequence of the Atomariini, I choose not to recognize any subtribes in the Atomariini, thereby suppressing the names Ephistemini and Salltiini.

The Atomariini contains a 4-branched polytomy at its base (Fig. 2) in EWC analysis and is resolved by SAW. The character conflict among these depends mainly on the phylogenetic placement of *Atomaria.* Trees that place *Atomaria* with the south temperate group (containing the genera *Paratomaria, Salltius,* and others) are one step shorter in tree length than those that show *Atomaria* as sister taxon to *Ootypus* and its relatives (based on SAW trees).

Cryptafricini: This monophyletic group is characterized by several unambiguous synapomorphies (CON1): punctation absent on prosternum (2), terminal antennomere 2x the length of the penultimate (4), absence of a median process on the mentum (14), procoxal cavity internally closed (45), surface of ventrite 5 with asperities (84-1), tarsomeres of male without modified setae (108). Concordant with these are: absence of ocular setae (24), width of mesosternal process 1/3 that of mesocoxa (65-1), meta-intercoxal process wider than long (76), absence of the spiculum gastrale in the female (88), ovipositor reduced (89), and apex of endophallus with a notch (91). Unambiguous synapomorphies that support the monophyly of Cryptafricini under CON2 are: 2, mandible without dorsal tubercles (10-0), presence of sensory pores on the mandible (12), 14, 45, 84-1, and 108. Concordant with these are: 24, 88, 89, and 91.

The tribe Cryptafricini is established here to include four previously undescribed genera occurring mainly in circumtropical regions of the world (see Taxonomic Treatment).

PROBLEMATIC CHARACTERS AND THEIR IMPACT ON PHYLOGENETIC STRUCTURE

In general, the problems encountered with cladistic characters regard the nature and definition of homology and the polarization of their states. These issues were considered previously in the Character Analysis whereas this section deals with particular characters that either have been weakly coded for the analysis, or have questionable optimizations on the resultant phylogenies.

I agree with Miyamoto (1985), Kluge (1988), and Kluge and Wolfe (1993) that robust hypotheses of relationships based upon evidential support (i.e., the number of characters that support a node) can only be ascertained by the inclusion of all potential data in a total evidence analysis. However, weakly formulated characters and poorly coded character states included in cladistic analysis could lead to weak or false phylogenetic conclusions. Also, characters with questionable character distributions that were originally included in an analysis may also lead to misleading conclusions. Therefore, I examine alternative phylogenies that are produced from experiments eliminating four characters from the data matrix and repeating the cladistic analyses (essentially down-weighting the questionable characters): absence or reduction of hind wings (102), loss of wing vein elements (106), diet (113), and inquilinism (114). I discuss in detail how these characters have been coded and the assumptions made by these codings.

Diet and Inquilinism: Because natural histories of most members of cryptophagids have not been studied in detail there is a paucity of behavioral characters useful for phylogenetic analysis. Inaccuracies that exist among these characters are associated with either a poor sample size and/or a weak formulation of character states. Without direct observations, diet (113) can be inferred by examination of gut contents (Leschen 1993). Diet character states for this analysis are based on two dissected specimens (male and female) for the majority of terminal taxa, and sometimes there is nothing contained within the midgut. Small sample sizes like these can produce misleading interpretations of diet (Leschen 1993). Also, recognition of a saprophagous diet is based upon relative quantities of unidentifiable material in the gut. If specimens are not immediately killed at time of collection and the preservative or killing agent has not entered the gut, decay in the midgut could destroy

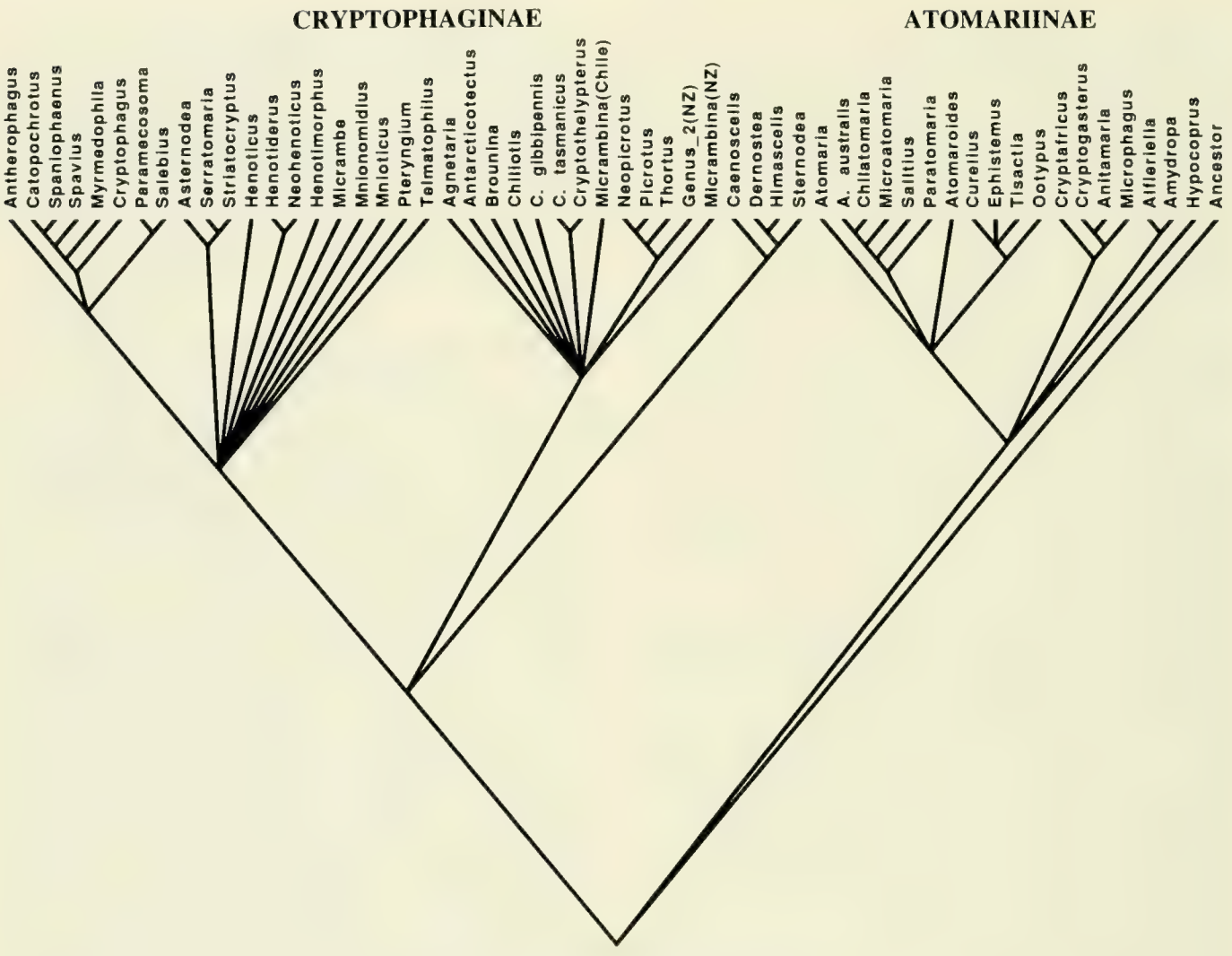


Fig. 9. Strict consensus tree (of 500 trees) of the phylogenetic relationships among members of Cryptophagidae with all characters of equal weight and hind wing character (102) removed.

information contained by contents (for example, enzymes and bacteria in the gut could destroy cell walls of original foods) that could also lead to wrong conclusions about diet. In summary, homologies of diet may be inaccurate because of poor sample size and misinterpretation of gut contents.

Problems associated with inquilinism (114) are coding; mainly, partitioning of this character into discrete homologous character states. Most specimens of the North American species *Hypocoprus tenuis* Casey have been collected from ant mounds, but specimens of the European *Hypocoprus lathridioides* Motschulsky have been collected in ant mounds, leaf litter, and animal dung. While the majority of species of *Cryptophagus* are free-living, some species have been collected in wasp and bee nests (some of these may not be obligate inquilines). In the case of *Hypocoprus*, I coded this taxon as fixed for ant inquilinism because the two species are both collected from ant nests. In the case of *Cryptophagus*, I coded this taxon as polymorphic for wasp/bee inquilinism because the majority of species do not occur in this habitat.

Moreover, character states for inquilinism may each reflect analogous states or need to be subdivided into additional states. For example, I have assumed that living in the nests of wasps and bees is homologous (coded as a single character state), when in fact the presence in *Bombus* nests (*Antherophagus*) is probably not homologous to the presence in wasp nests (some members of *Cryptophagus*) and represents independent colonization events. Likewise, those species that are ant inquilines occur among a variety of ant genera, suggesting that the different hosts may represent separate colonization events. This typological approach to character coding essentially forces the variable behavioral information into discretely-coded data necessary for cladistic analysis (W. Wcislo, personal communication).

Under the dictum of total evidence exclusion of the behavioral characters does not seem warranted because these

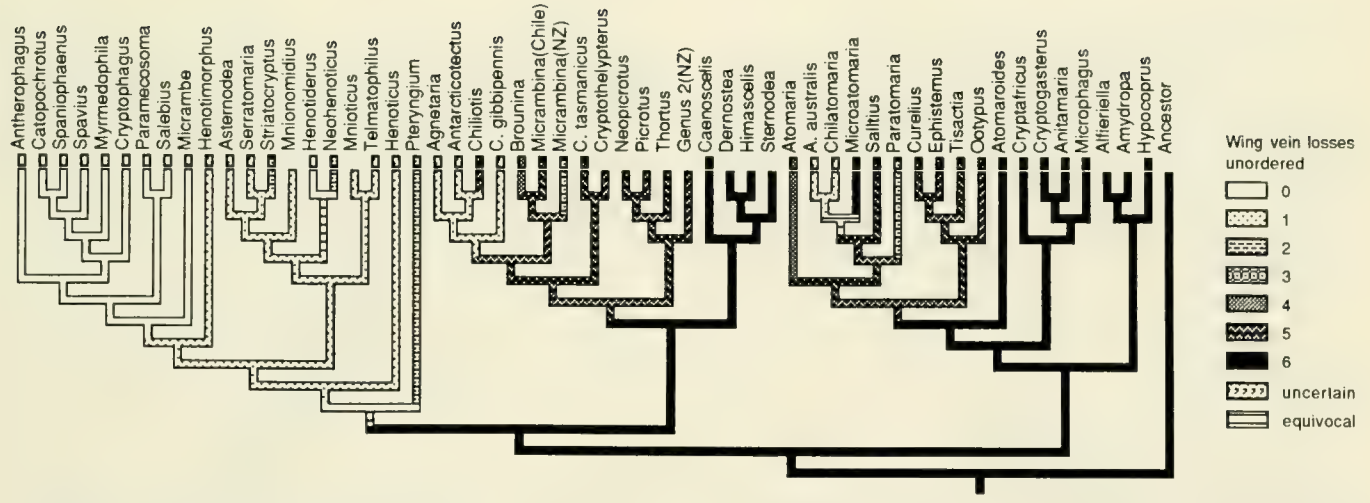


Fig. 10. Hind wing vein losses and gains (106) mapped onto one of the cladograms produced by successive approximations weighting. Character states as follows: (0) All wing veins present; (1) MP_3 absent; (2) CuA_{3+4} absent; (3) MP_3 and CuA_{3+4} absent; (4) MP_4+CuA_1 and MP_3 absent; (5) MP_4+CuA_1, MP_3, and CuA_{3+4} absent; (6) CuA_{3+4}+AA_{1+2}, MP_4+CuA_1, MP_3, and CuA_{3+4} absent.

characters may provide data supporting phylogenetic pattern. However, due to possible inaccuracies defining character states for diet and inquilinism, I have eliminated these two characters from the data matrix and repeated the cladistic analysis: With equal weighting for all characters, this produced over 500 trees (TL = 393, CI = 0.366, RI = 0.746) shown as a strict consensus tree (Fig. 7). Comparisons made with those EWC trees from the original analysis (Fig. 1) show different patterns of resolution, especially in resolving the messy basal polytomy of caenosceline and cryptosomatuline taxa. SAW analysis resulted in nine trees in two iterations, and these differ from the total evidence trees by the arrangement of taxa among Cryptophagini (shown as a strict consensus tree in Fig. 8). This exclusion experiment resulted in no change in phylogenetic pattern among members of the Atomariinae; however, lineages of Cryptophaginae are affected. The following consistencies among the SAW trees are: *Mnioticus* + *Telmatophilus* are sister taxa to *Henotiderus* + *Neohenoticus*, *Mnionomidius* is placed at the base of the *Cryptophagus*-group, *Salebius* + *Paramecosoma* are sister taxa to *Antherophagus*, and *Myrmedophila* is placed one step below the polytomy among the *Cryptophagus*-group. The changes among members of the *Cryptophagus*-group are expected, because the resolutions among these taxa in the total evidence analysis are largely based on behavioral characters. Therefore, behavioral data have a significant impact on our ability to perceive phylogenetic pattern and because of tenuous character formulations and poor sample sizes for behavioral characters, branching sequences that depend on behavioral characters for support are suspect.

Hind wing reduction or loss: There is no reason why discrete (fixed) characters that may occur as polymorphisms among some terminal taxa should be eliminated from an analysis *a priori* if they contain potential phylogenetic information. Aptery and brachyptery are widespread in most lineages of beetles and occur either as fixed or polymorphic characters within a species or genus. Because of the widespread occurrence of this phenomenon, and perhaps the lability of this character as a response to heterogenous or stable environments (see Roff 1990), some beetle systematists have fervently argued during personal discussions that this character should not be used and should be eliminated *a priori* from a cladistic analysis. These arguments are based upon a general lack of clarity between pattern and process and epistemological issues relating to discovery method. Hind wing loss is influenced by genetic and developmental processes (e.g., programmed death of cell lineages is not necessarily "simple" or "plastic") and should be treated as other phenotypes that vary discretely among terminal taxa.

I have included hind wing reduction or loss (HWL, 102) in the analysis because it has been fixed in several genus-level taxa (*Mnionomidius, Mnioticus, Cryptothelypterus, Neopicrotus, Picrotus, Thortus, Salltius, Alfieriella, Amydropa, Dernostea, Sternodea, Himascelis*, and genus 2). Moreover, this character supports some of the relationships among HWL taxa, usually corroborative with other characters. When this character is optimized onto some of the phylogenies its distribution, under ACCTRAN, implies that wings have been lost and regained during phylogenetic history.

A closer look at Cryptosomatulini and Caenoscelini (Figs. 4, 6) show the phenomenon of loss and regain of hind wings. Based on ACCTRAN character optimization, HWL is placed at the base of the these (CON1, Fig. 6a), and a hind wing is regained near the base of Cryptosomatulini and in *Caenoscelis* and lost again in *Cryptothelypterus* (Fig. 4). In an alternative tree (CON2), HWL is placed at the base of Caenoscelini (Fig. 6), a clade containing *Thortus*, genus 2, *Picrotus*, and *Neopicrotus*, and *Cryptothelypterus*. Because the character is polymorphic among species of *Caenoscelis*, the character distribution implies that hind wings are regained in winged species of *Caenoscelis*. I am unaware of reports of hind wings regained among flightless beetle lineages and it seems unlikely that this pattern is true among members of

the Cryptosomatulini and Caenoscelini. However, the lack of evidence for regained wings may be the result of a failure to use comprehensive cladistic analysis necessary to discover this pattern. Evidence hinting at the regaining of hind wings is that cryptosomatulines and members of *Caenoscelis* do not have a "full" complement of the wing veins present among some other members of Cryptophagidae (Cryptophagini) and other Cucujoidea. However, reduction of wing vein elements among Cryptophagidae is very widespread (see below), and a reduced complement of wing veins is a weak argument for reacquisition of hind wings.

The occurrence of HWL and regains among Cryptophagini may be attributed to the codings of polymorphisms in terminal taxa. Polymorphic taxa are not fully recognized by character mapping and tree building algorithms and the polymorphisms are treated in the same way as missing values (Nixon and Davis 1991). If Caenoscelini and Cryptosomatulini are sister taxa (CON1), then HWL evolved three times (once each at the base of Caenoscelini + Cryptosomatulini and in members of *Cryptothelypterus*), and hind wings are regained in some members of *Caenoscelis*, one step from the base of Caenoscelini (Fig. 4, 6). In contrast, if Cryptosomatulini is the sister taxon to Cryptophagini (Fig. 6, CON2), then HWL evolved three times and hind wings have been regained once in some members of *Caenoscelis*. These interpretations are equally parsimonious, each requiring a total of four steps. On the other hand, if polymorphisms are coded as separate taxa as prescribed by Nixon and Davis (1991), *Caenoscelis* is represented as two terminal taxa, one with hind wings and one with HWL. The results show that hind wings are regained in winged *Caenoscelis* as before. Another solution is to codify the ground state as that present in the outgroups and not recognize the polymorphism. Use of this option (i.e., *Caenoscelis* is coded as winged) results in HWL having evolved three times, which is seemingly more parsimonious, but of course ignores those species of *Caenoscelis* that have HWL. If DELTRAN character optimization is employed, which optimizes characters as parallelisms, using the original codifications in the data matrix then HWL is not a synapomorphy of Caenoscelini. This pattern is more consistent with the idea that HWL is convergent and hind wings are not regained. Because the relationships among the 20 or so species of *Caenoscelis* are unknown, HWL or hind wing reacquisition may have occurred more times than that implied by the oversimplified coding schemes for polymorphisms in my coarse-grained analysis.

Changing the assumptions about transformations between states provide insight about the evolution of HWL. When treated as a Dollo character (see Farris 1977, and Maddison and Maddison 1992 for how it is treated in MacClade), HWL can only arise once, but multiple regains is permitted. When Dollo option is activated for HWL, tree length increases by 9 steps (based on SAW trees) and hind wings are reacquired 10 times. When HWL is treated as an irreversible character (Camin and Sokal 1965, Maddison and Maddison 1992), multiple gains of HWL is allowed, but hind wing reacquisition is impossible. When the irreversible assumption is made in MacClade there is no change in tree length and HWL is equivocal at the base of Caenoscelini. This is similar to the results that occur when DELTRAN character optimization is in effect, except that HWL is equivocal at the base of Caenoscelini. If it is assumed that hind wing reacquisition is impossible or a rare event, then treating this character as irreversible is more consistent with this hypothesis.

When HWL (102) is removed from the cladistic analysis, 500 trees are produced with the following tree statistics: TL = 401, CI = 0.369, RI = 0.742. A strict consensus tree (Fig. 9) shows resolution among cryptophagine clades with a trichotomy among the three tribes. SAW analysis (requiring two iterations), produced nine trees, all of which are the same as those produced in the original analysis (Fig 2). Despite the implications for the evolution of hind wing loss, the exclusion of this character has little effect on tree structure (among SAW trees) suggesting that the relationships it supports and the evolutionary pattern of hind wing loss are supported by other character distributions.

Hind wing vein losses: Reduction in wing vein elements (106) is very variable among members of Cryptophagidae and consists of seven character states. Based on the branching patterns of the phylogenies (Fig. 10), the loss or absence of the majority of wing vein elements (106-6) is present at the base of the cladogram implying, therefore, that this character state may be in the groundplan of Cryptophagidae. This is curious because a larger complement of wing veins is present among some members of the Cryptophaginae, five or six steps from the base of the cladogram among SAW trees. One reason for this character optimization may be that those taxa polymorphic or fixed for HWL (including the outgroup) are coded as unknown or polymorphic for this character. As previously discussed, data entries coded as polymorphic or unknown are computationally ignored by tree building and character mapping algorithms (Nixon and Davis 1991, Platnick et al. 1991).

Most members of the *Cryptophagus*-group have a full complement of wing veins present (106-0), and based on the phylogenies, this type of wing venation is derived among Cryptophagidae (Fig. 10). A similar phenomenon exists among Atomariini, although the total number of wing veins is less. This is interesting because the larger complement of wing veins that occurs in Cryptophagidae is also present in other members of Cucujoidea (e.g., Cucujidae, Silvanidae). The variation in the wing vein patterns among lower Cucujoidea is highly variable and includes repeated patterns of "losses" in wing vein elements (assuming a larger complement of wing veins is primitive). This poses an interesting problem for evolutionary biologists and cucujoid systematists because if a full complement of wing veins is present in the groundplan of Cucujoidea, then regaining of a full complement among clades with wing vein losses may be atavistic. To analyze this character in more detail I recommend the following: 1) Study the wing veins among lower Cucujoidea to determine if those present in Cryptophagini are indeed homologous to those in other groups (e.g., vari-

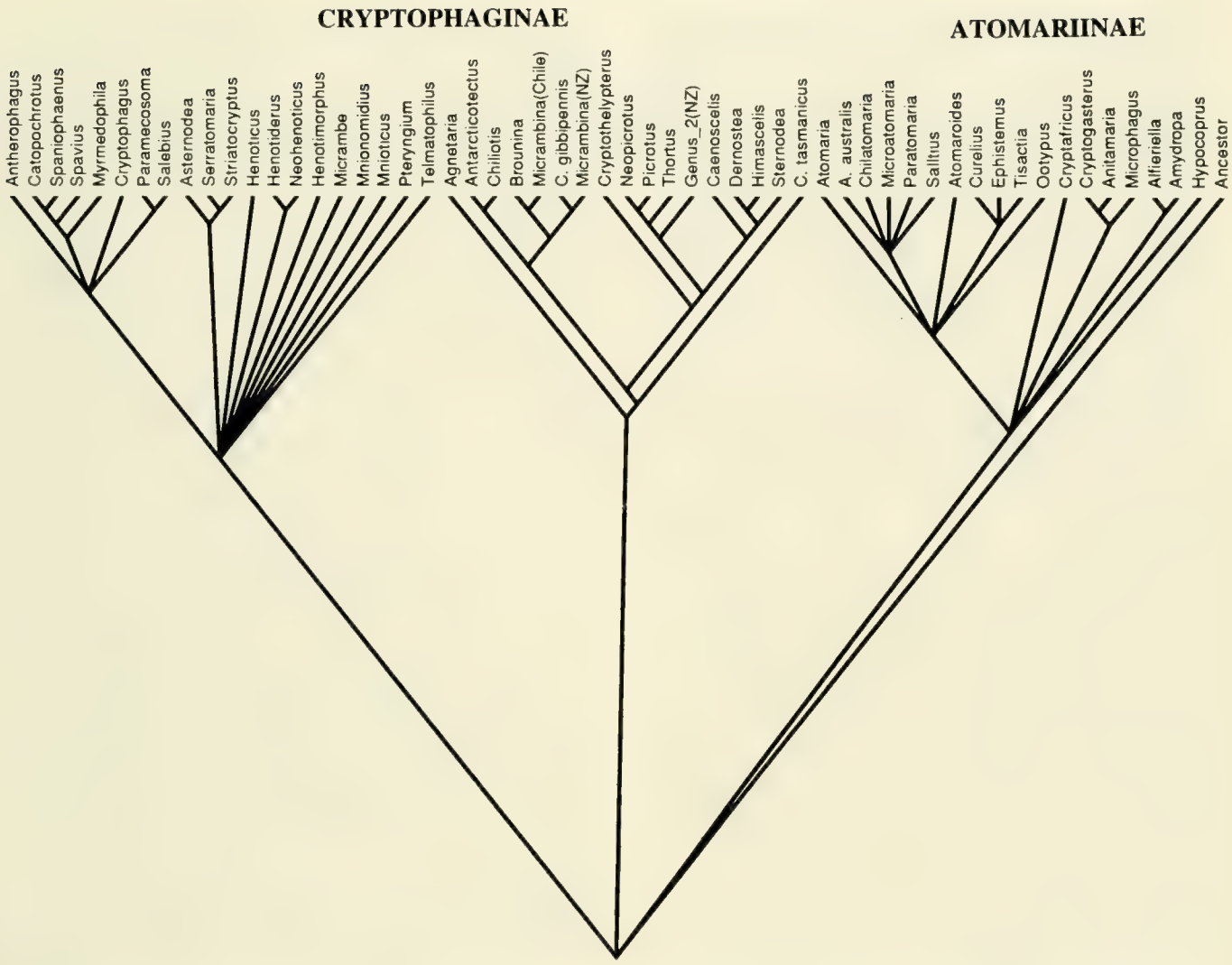


Fig. 11. Strict consensus tree (of 95 trees) of the phylogenetic relationships among members of Cryptophagidae with all characters of equal weight and wing vein character (106) removed.

ation in number, position and lengths may support or refute hypotheses of ancestry or convergence). 2) Order the various character states and examine the effects on resulting phylogenetic patterns. 3) Adapt Transformation Series Analysis (Mickevich 1982, Mickevich and Weller 1990) and other methods (Lipscomb 1992) to recode missing entries for terminal taxa, thereby inferring possible states among ancestors. 4) Analyze the phylogenetic relationships of lower Cucujoidea to determine immediate outgroup to repolarize character states and, perhaps, root the tree at a different location. Dealing with character states of wing veins will prove to be one of the most interesting and vexing problems of character analysis in the superfamily, as it has been for the entire Coleoptera (Kukalova-Peck and Lawrence 1993).

500 trees (TL = 390, CI = 0.367, RI = 0.744) are produced (Fig. 11) when character 106 is removed from the data matrix and the cladistic analysis is repeated. SAW with three iterations results in nine trees (Fig. 12). This experiment demonstrates that wing vein losses definitely support some of the relationships among Atomariinae and Cryptophaginae. Among the SAW trees, *Mnionomidius* is placed at the base of the tree, *Henotimorphus* is removed from the *Cryptophagus*-group, and *Henoticus* placed higher into the *Henoticus*-group among the Cryptophagini, Caenoscelini are placed within Cryptosomatulini, and *Ootypus* and its relatives are shifted as a sister group to *Atomaria* among Atomariini. Mapping the character states of wing vein loss onto these trees does not result in a significantly different transformation series—a larger number of wing veins is derived.

FAMILY CRYPTOPHAGIDAE

Cryptophagidae Kirby, 1837:vii. Type genus: *Cryptophagus* Herbst, 1792.
Hypocopridae Reitter, 1879:74. Type genus: *Hypocoprus* Motschulsky, 1839. Considered at one time as a family by Crowson (1955).
Catopochrotidae Reitter, 1889:79. Type genus: *Catopochrotus* Reitter, 1889.

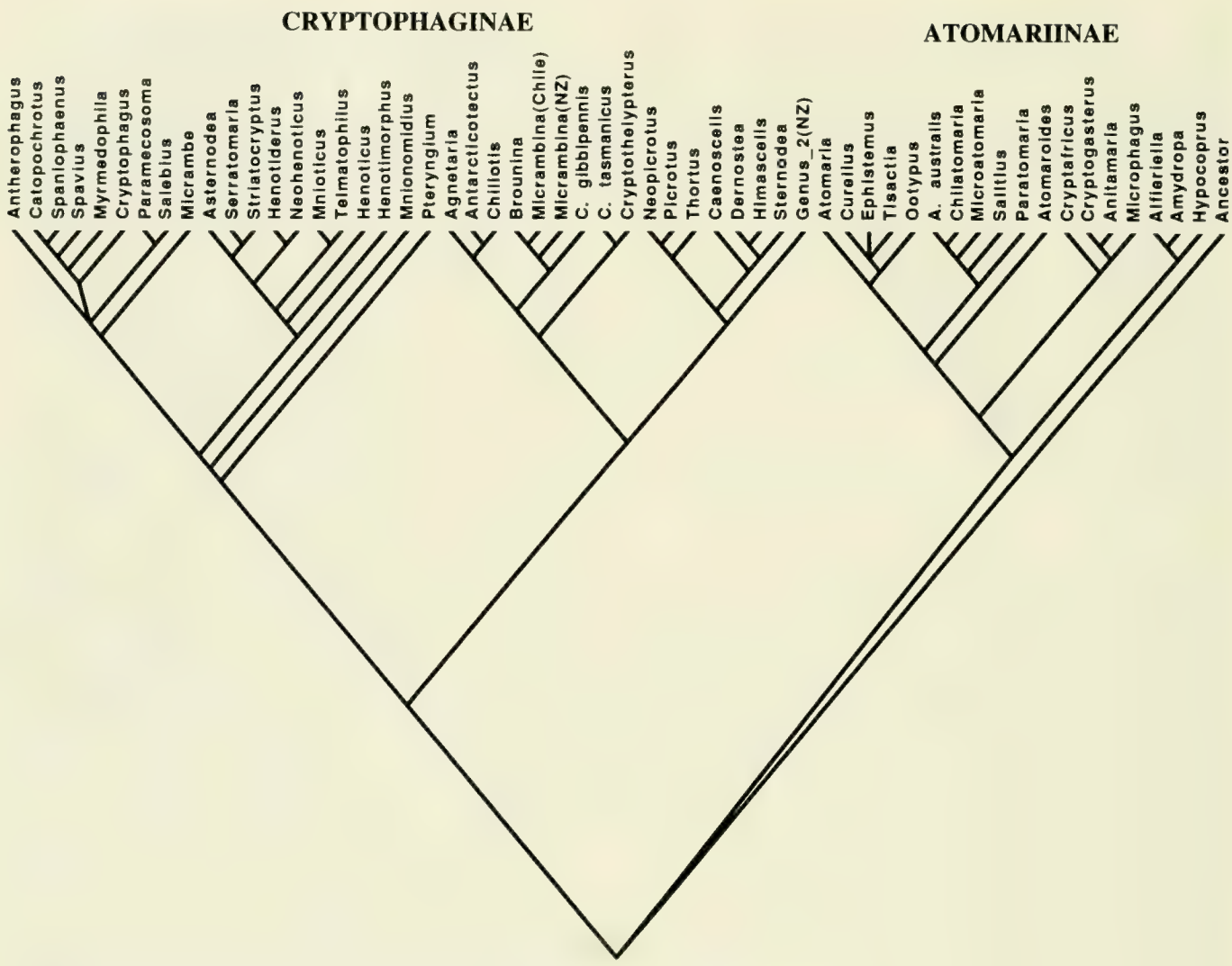


Fig. 12. Strict consensus tree (of nine trees) of the phylogenetic relationships among members of Cryptophagidae with successive approximations weighting of characters with wing vein character (106) removed.

Diagnosis— Antennal insertions exposed in dorsal view; mandible without a deep cavity or mycangium; tentorium without median tendon; prothorax with or without (in Hypocoprini) well developed marginal bead (present in basal half only among some Atomariini); mesocoxal cavity closed laterally by the sternum; ventrite 1 longer than remaining ventrites (ventrites equal in length among *Mnioticus*, *Henotiderus*, *Serratomaria*, *Striatocryptus* and *Hypocoprus*); epipleuron distinct in basal half (distinct beyond basal half in some species); punctation of elytron confused (striate in *Striatocryptus* and some *Henotiderus*).

Description.— Body length 0.8 - 5.2 mm. Body form elongate and parallel-sided, moderately flattened or highly convex, oval, or round. Body color various, most dark, light, or red brown. Body setae long or short, decumbent, apressed, suberect, erect. Glandular ducts present in various parts of the body (Atomariini, Cryptafricini, and Cryptophagini).

Head longer than wide, retracted into thorax (especially in *Catopochrotus*), with or without a short neck, with or without line on vertex, without stridulatory files (except for some species of *Atomaria*), with or without subgenal spines; frons without lateral tubercles (except in some Atomariini); antennal grooves present in *Ephistemus*, with or without gular suture. Eyes well developed and finely faceted (reduced to few facets in some brachypterous forms), with or without ocular setae. Clypeus more or less quadrate, with or without frontoclypeal suture. Antennal club 3-segmented (1- or 2-segmented in some members of Caenoscelini and Atomariinae), antenna inserted into a small or large concavity; antennomeres of variable shapes and sizes; funicle curved and conical or barrel shaped. Mandible with well developed mola, incisor apex, and prostheca, dorsal tubercles present or absent, deep cavity or mycangia absent. Maxilla brushlike with well developed marginal setae and apical spines, maxillary palpomeres more or less subequal to each other. Labium with mentum wider than long, with or without transverse ridge or line, with or without middle process; labial palpus 2-segmented with basal palpomere subequal to apical palpomere (Cryptophaginae and Cryptosomatulini) or basal palpomere larger in width than apical palpomere (Atomariinae and Caenoscelini). Tentorium with anterior arms fused or separate, posterior part bar or straplike, without anterior median tendon. **Prothorax** with well developed marginal bead (absent in Hypocoprini and present in basal half only in some Atomariini); side with or without marginal teeth or processes or angularities. Pronotal disc with (Cryptophagini) or without basal pits; with depressions (in some Cryptosomatulini). Hypopleuron without an-

tennal grooves (except some Caenoscelini and *Ephistemus*); with or without notch above procoxa. Prosternal process well developed (length less than anterior portion in some Atomariinae); vaulted or not (flat). Procoxae rounded and separate; procoxal cavities externally open or closed; internally open or closed. **Mesosternum** with or without procoxal rests. Mesepimeron with or without distinct pit, fused with mesosternum in *Alfieriella* and *Amydropa*. Mesocoxal cavities closed laterally by sterna. Mesometasternal articulation with either a double knob (most Cryptophaginae) or lateral processes (Atomariini) or unmodified. Metasternum elongate or short (in some HWL forms); with or without longitudinal line. Metendosternite with a broad stalk; most with basal plate transverse with well developed arms; with anterior tendons present (without in some HWL forms), approximate or distant. **Abdomen** with 5 freely articulated ventrites. Ventrite 1 longer or equal in length to remaining ventrites; with or without metasubcoxal lines. Intercoxal process moderately broad, longer than wide in some species (*Striatocryptus*). Ventrite 5 with modified setae (Caenoscelini) or asperites (Cryptafricini). **Elytra** completely covering abdomen (tergite 7 exposed in some species); punctation confused or arranged into rows (some *Henotiderus* and *Striatocryptus*); epipleuron distinct in basal half (distinct beyond basal half in some *Tisactia*, some *Antherophagus*, and some Cryptafricini). Wings with up to 5 major veins; cell formed by the merging of veins CuA_2 and CuA_{3+4}+AA_{1+2} (some Cryptophagini); with or without basal binding patch. **Legs** relatively long; length of trochanter about 1/4 that of femur; tibia parallel-sided or club shaped, most with 2 apical spines (0 or 1 may be present); tarsi 555 in female, 554 or 555 in male, 444 in both sexes (in *Cryptafricus* and *Atomaroides*).

Male.— Spiculum gastrale with long anterior strut (most Cryptophaginae) or broad (most Atomariinae); asymmetrical in some Atomariini. Orientation of aedeagus vertical or horizontal in body cavity, bilaterally symmetrical or not in some Atomariini; parameres separate or fused (most Atomariinae), internal sac complex or not; dorsal arms of tegmen narrow or joined at their apices or not, or broadly fused; flagellum present or not.

Female.— Ovipositor well developed or reduced. Spermatheca usually c-shaped; spermathecal duct sclerotized or not, coiled or straight.

Discussion.— I recognize 51 genera (43 are reviewed here) placed among two subfamilies and six tribes (see Appendix). There are additional undescribed genus level taxa (one in Cryptophagini from Kenya [known from a single specimen] and several in the southern hemisphere Cryptosomatulini) not treated in this study.

KEY TO THE GENERA AND HIGHER TAXA OF CRYPTOPHAGIDAE

The following key includes all genera examined for this study except for members of the tribe Cryptosomatulini. Because cryptophagids are small in size it is important that specimens be identified with high magnification and some difficult taxa must be dissected for exact determination. Although I have relied on many characters that do not require dissection the first couplet has characters that are variable and the exceptions are indicated parenthetically. The genus *Henoticus* keys out in two places.

Note that languriids have a complete elytral epipleuron and the first ventrite is equal in length to the remaining ventrites.

1. Tarsal formula of male 554 (555 in *Telmatophilus, Mnioticus*, and some species of *Striatocryptus, Henoticus, Cryptophagus* and *Caenoscelis*); subgenal spines usually well developed (Figs. 15, 140, 146); procoxal cavities internally closed (Figs. 39-41, 135); double knob present at the meso-metasternal articulation (Fig. 73, some genera with a single knob); parameres articulated (Figs. 11, 114-118, fused in some species of *Caenoscelis*) . . . . . .Cryptophaginae 2
— Tarsal formula of male 555 (444 in *Cryptafricus* and *Atomaroides*); without subgenal spines (Figs. 13, 134, except for some members of *Alfieriella* [Fig. 14]); procoxal cavities internally open (Fig. 37, closed in Cryptafricini); without double knob at meso-metasternal articulation (Fig. 168); without articulated parameres (Fig. 105, present in *Alfieriella* and *Amydropa*) . . . . . .Atomariinae 27
2. Hypomeron with notch above coxal articulation (Figs. 40, 41); pronotum (Figs. 47, 48, 50-54) with lateral margin serrate, with or without angularity, basal pits or groove; conspicuous glandular ducts present in body, without microtubules. Distributed mainly in the Holarctic . . . . . .Cryptophagini 7
— Hypomeron without notch above coxal articulation (Figs. 39, 135); pronotum unmodified in most species, if angularity present, it is above the lateral marginal bead and spiracle on abdominal segment 7 is modified; without conspicuous glandular ducts, with or without microtubules. Distributed worldwide 3
3. Frons with boss (as in Fig. 133); head without gular sutures (as in Fig. 13); serrations present on incisor lobe of mandible (Figs. 18, 167); microsculpture of prescutum elongate variolate (Fig. 91); orientation of aedeagus vertical. Distributed in holarctic and circumtropical regions . . . . . .Caenoscelini 4
— Frons without boss; head with gular sutures (as in Fig. 16); incisor lobe of mandible without serrations; microsculpture of prescutum variolate (Fig. 90); orientation of aedeagus horizontal in most species. Most species distributed in south temperate regions . . . . . .Cryptosomatulini (not keyed to genera)
4. Body elongate; pronotum parallel-sided; prosternal process not vaulted; antennal club 3-segmented . . . . . .*Caenoscelis* (Fig. 189)
— Body oval; pronotum widest at base (as in Fig. 193); prosternal process vaulted (Figs. 36, 144); antennal club 2- or 1-segmented 5
5. Hypomeron without antennal groove and transverse fovea; antennal club usually 2-segmented . . . .*Sternodea*
— Hypomeron without antennal groove and transverse fovea (Figs. 36, 144) 6
6. Antennal club 2-segmented . . . . .*Himascelis* (Fig. 193)
— Antennal club 1-segmented . . . . . .*Dernostea*
7. Body form limuloid; antenna clavate (Fig. 33) . . . . . .*Catopochrotus* (Fig. 178)
— Body form not limuloid; antenna clubbed 8
8. Pronotum with three lobes or undulations (Fig. 42) . .9
— Pronotum without three lobes (two may be present) 10
9. Pronotum without basal pits; without metasternal pit; occurs in Europe and Asia . . . . . .*Paramecosoma*

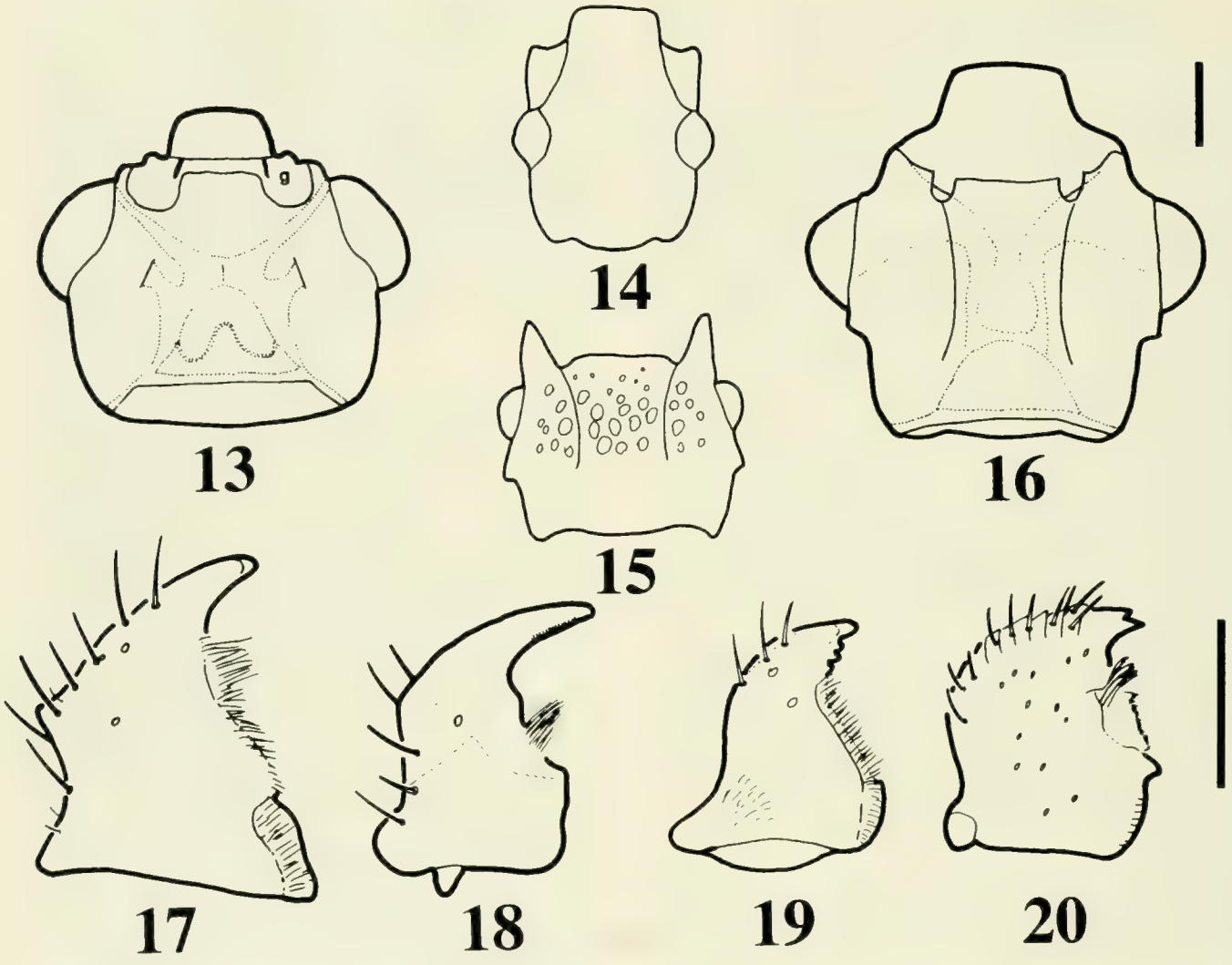


Fig. 13-20. Heads and mandibles of Cryptophagidae. **13,** *Anitamaria* sp. (Australia), ventral view of head. **14,** *Alfieriella denticulata*, dorsal view of head. **15,** *Neopicrotus peckorum*, ventral view of head. **16,** *Micrambina* sp. (New Zealand), ventral view of head. **17,** *Cryptophagus* sp. (North America), dorsal view of left mandible. **18,** *Sternodea* sp. (Mexico), dorsal view of left mandible. **19,** *Chilatomaria hillersae*, dorsal view of left mandible. **20,** *Cryptogasterus lawrencei*, dorsal view of left mandible. (Scale bars = 0.1 mm, g = glandular duct).

— Pronotum (Fig. 42) with basal pits; with metasternal pit; occurs in western North America . . . . . .*Salebius* (Fig. 188)

10. Pronotum with sublateral line (Figs. 43, 142, 145) . . . . . .*Henotiderus* (Fig. 176)

— Pronotum without sublateral line 11

11. Elytron with punctate stria . . . . . .*Striatocryptus*

— Elytron without punctate stria 12

12. Pronotum with a distinct angularity (Figs. 50, 53) or enlarged region in the anterior portion of the marginal bead 13

— Pronotum without a distinct angularity or widened region in the anterior portion of the marginal bead .18

13. Male with a distinct clypeal notch (Figs. 34, 175); body color golden-brown or yellow; usually in *Bombus* nests or on flowers . . . . . .*Antherophagus* (Fig. 174)

— Male without clypeal notch; body color variable; rarely present in *Bombus* nests or on flowers 14

14. Anterior margin of pronotum emarginate (as in Fig. 40) such that the head is retracted into the prothorax 15

— Anterior margin of pronotum not or slightly emarginate (as in Fig. 41) such that the head is not retracted into the prothorax 16

15. Dorsum shining, not reticulate, punctation normal; antenna thin, club flattened; not found in *Formica* ant nests . . . . . .*Spaniophaenus* (Fig. 182)

— Dorsum opaque, strongly reticulate with very fine points; antenna thick, club not flattened; found in *Formica* ant nests . . . . . .*Spavius* (Fig. 186)

16. Color of body red-brown; setae of elytron apressed; present in *Formica* ant nests; pronotal margin with 2

glandular ducts; found in western North America ..... *Myrmedophila* (Fig. 190)

— Color of body variable; setae of elytron apressed in a few species; not found in *Formica* ant nests; pronotal margin with one, two, or three glandular ducts 17

17. Pronotum usually with a middle tooth, if not, pronotal margin with two or three glandular ducts; male with star-shaped glandular ducts (Fig. 163) .... *Cryptophagus* (Fig. 180)

— Pronotum without a middle tooth; pronotal margin with one glandular duct; male without star-shaped glandular ducts ..... *Micrambe* (Fig. 184)

18. Pronotal margin without distinct serrations 19

— Pronotal margin with distinct serrations 20

19. Basal pits of pronotum connected by a groove (as in Fig. 47); prosternal process with glandular duct; ventrite 1 longer than remaining ventrites .... *Henoticus* (in part, Fig. 181)

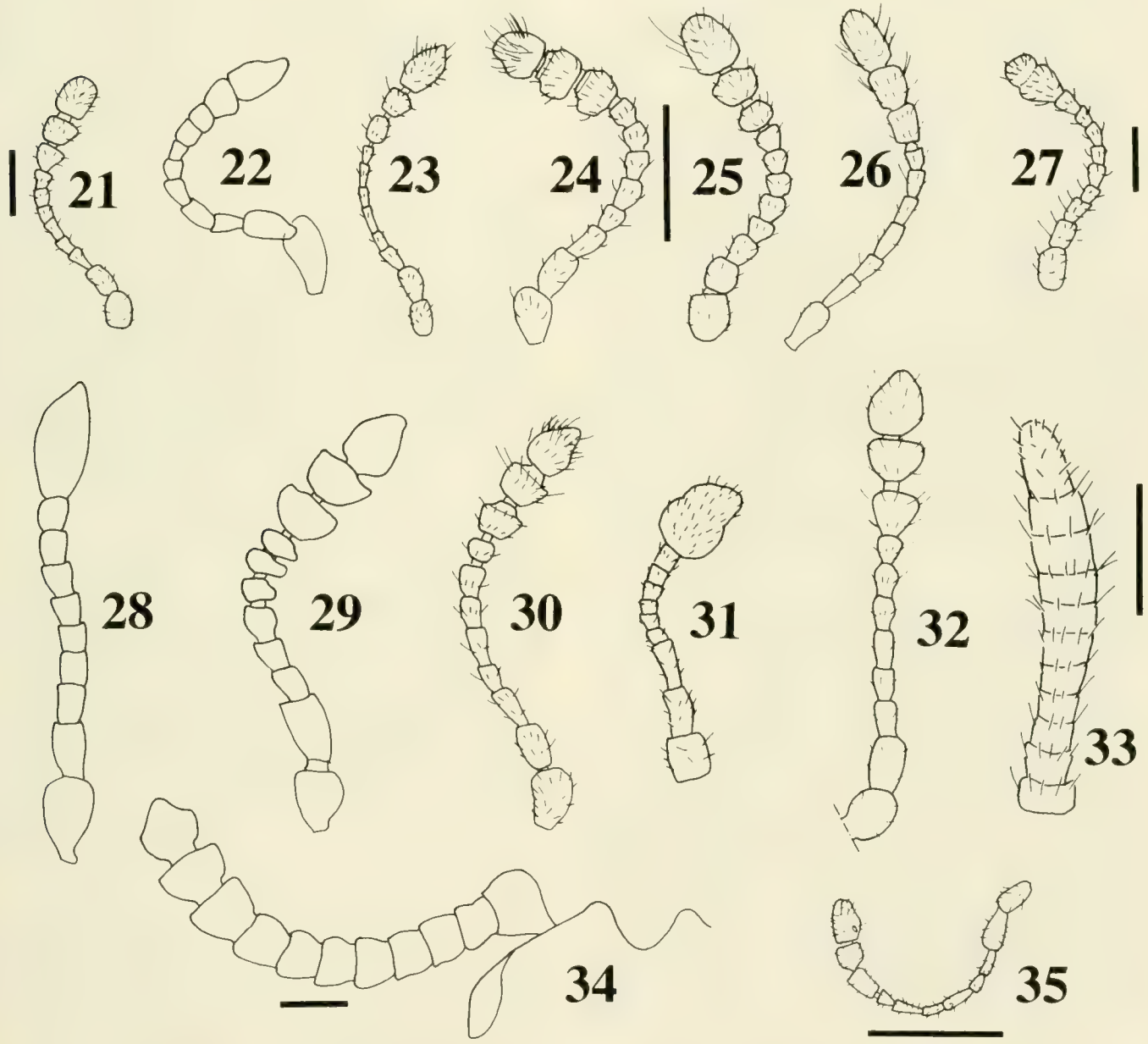


Fig. 21-35. Antennae of Cryptophagidae. **21,** *Asternodea loebli.* **22,** *Cryptafricus leleupi.* **23,** *Anitamaria thayerorum.* **24,** *Chilatomaria hillersae.* **25,** *Neopicrotus peckorum.* **26,** *Striatocryptus wilkinsoni.* **27,** *Microatomaria hintoni.* **28,** *Alfieriella denticollis.* **29,** *Amydropa anophthalma.* **30,** *Paratomaria crowsoni.* **31,** *Dernostea tanakai.* **32,** *Neohenoticus palmerae.* **33,** *Catopochrotus crematogastri.* **34,** *Antherophagus* sp. (male, North America). **35,** *Microphagus johnsoni.* (Scale bars = 0.1 mm).

— Basal pits of pronotum not connected by a groove; prosternal process without glandular duct; ventrite 1 equal to remaining ventrites ..... *Mnioticus* (Fig. 185)
20. Tarsal formula 555 in male; tarsal segments strongly lobed beneath; found on aquatic plants (usually *Sparganium* and *Typha*) ..... *Telmatophilus*
— Tarsal formula 554 in male; tarsal segments not strongly lobed beneath; not associated with aquatic plants 21
21. Pronotal margin irregularly serrate (as in Fig. 43) .. 22
— Pronotal margin regularly serrate (as in Fig. 52) ... 24
22. Pronotum somewhat angulate and widest in middle; found in Chile ..... *Neohenoticus* (Fig. 191)
— Pronotum more or less parallel-sided or evenly-arcuate; found in Asia 23
23. Pronotal serrations grouped into three distinct regions; ventrite 1 longer than remaining ventrites ..... *Henotimorphus*
— Serrations continuous; ventrite 1 not longer than remaining ventrites ..... *Serratomaria* (Fig. 192)
24. Prosternal process vaulted (Fig. 64); glandular ducts saccular (Fig. 74) ..... *Asternodea* (Fig. 177)
— Prosternal process flat; glandular ducts not saccular 25
25. Eyes reduced to a few facets; without hind wings ..... *Mnionomidius* (Fig. 183)
— Eyes well developed; hind wings present in most species 26
26. Body dorsoventrally compressed; mesosternal process greater in width than mesocoxa; without abdominal glandular ducts ..... *Pteryngium* (Fig. 187)
— Body not dorsoventrally compressed; mesosternal process equal in width to mesocoxa; with abdominal glandular ducts ..... *Henoticus* (in part, Fig. 181)
27. Pronotal bead completely absent; without frontoclypeal suture (Fig. 14) ..... Hypocoprini 28
— Pronotal bead present; with frontoclypeal suture .. 30
28. Antennal club 1-segmented (Fig. 28); elytral humeri strongly toothed (in described species) ..... *Alfieriella* (Fig. 196)
— Antennal club 3-segmented (Fig. 29); elytral humeri not strongly toothed 29
29. Head subparallel behind eyes, with conspicuous temples ..... *Hypocoprus* (Fig. 195)
— Head abruptly narrowed behind eyes, without temples ..... *Amydropa* (Fig. 137)
30. Tibia without apical spines (Fig. 155); coxal cavity internally closed (Fig. 57); ventrite 5 with small asperities (Fig. 80, 153) ..... Cryptafricini 31
— Tibia with apical spines; coxal cavity internally open (Fig. 37); ventrite 5 without asperities .. Atomariini 34
31. Tarsal formula 444 ..... *Cryptafricus* (Fig. 201)
— Tarsal formula 555 32
32. Terminal antennomere about as long as wide (as in Fig. 25), its length scarcely two times that of penultimate; found in gasteromycete fungi in eastern Australia ..... *Cryptogasterus* (Fig. 203)
— Terminal antennomere longer than wide (as in Fig. 23), its length two times that of penultimate; not present in gasteromycete fungi 33
33. Pronotal lateral margin with a visible angularity ..... *Microphagus* (Fig. 206)
— Pronotal lateral margin without a visible angularity (it is absent or hidden from view by a cluster of setae) ..... *Anitamaria* (Fig. 200)
34. Pronotum with a wide marginal bead (Fig. 55); tarsal formula 444 ..... *Atomaroides*
— Pronotum with a narrow marginal bead; tarsal formula 555 35
35. Prosternal process vaulted and bearing two parallel lines (as in Fig. 36) 36
— Prosternal process flat and without parallel lines ... 38
36. Body elongate and moderately convex ..... *Tisactia* (Fig. 207)
— Body oval and highly convex (Fig. 208) 37
37. Antennal grooves present on the subgena and prosternum ..... *Ephistemus*
— Antennal grooves absent ..... *Curelius*
38. Body oval and highly convex; scutellum weakly transverse ..... *Ootypus* (Fig. 208)
— Body usually elongate and moderately convex (Figs. 197-199, 202); scutellum strongly transverse 39
39. Hypomeron with notch near procoxal cavity (Fig. 37); mesosternal glandular ducts without callus (as in Fig. 54); found mainly in northern temperate regions ..... *Atomaria* (Figs. 197, 202)
— Hypomeron without notch present near procoxal cavity; if notch is present, then mesosternal glandular ducts open onto a callus (Fig. 152); found in southern temperate regions 40
40. Elytral setae biseriate and erect, almost as long as protarsus ..... *Salltius* (Fig. 209)
— Elytral setae uniseriate and apressed, shorter than the protarsus 41
41. Tarsomeres strongly lobed; glandular ducts of mesosternum not opening onto a callus (Fig. 154) ..... *Paratomaria* (Fig. 199)
— Tarsomeres not strongly lobed; glandular ducts of the mesosternum opening onto a callus or not 42
42. Antennal club 3-segmented ..... *Chilatomaria* (Figs. 198, 204)
— Antennal club 2-segmented (Fig. 27) ..... *Microatomaria* (Fig. 205)

SUBFAMILY CRYPTOPHAGINAE

Cryptophaginae Kirby, 1837:vii. Type genus: *Cryptophagus* Herbst, 1792.

Diagnosis.— Head without frontoclypeal suture. Subgenal spine present (absent in some members). Transverse line on vertex of head (absent in *Catopochrotus* and *Picrotus*). Meso-metasternal articulation with double knob (absent in some members). Aedeagus with arms of tegmen narrowly fused or separate apically (broadly fused in *Striatocryptus*); articulated parameres present. Tarsal formula of male 554 (555 in some species).

Description.— Conspicuous glandular ducts present in the body (absent in Caenoscelini and Cryptosomatulini); microglandular ducts present in Cryptosomatulini. Head with frontoclypeal suture absent (present in one species of *Serratomaria*); width of palpomere 1 subequal to that of palpomere 2 (Cryptosomatulini and Cryptophagini) or greater than that of palpomere 2 (Caenoscelini); transverse ridge or line present on mentum (absent in *Henotiderus*); subgenal spine present (absent in some Cryptophagini); gular sutures present (absent in Caenoscelini and some Cryptophagini); transverse line on vertex of head present (absent in *Catopochrotus* and *Picrotus*); anterior arms of tentorium separate; posterior portion of tentorium straight and broad. Pronotum with lateral margin modified with serrations, a pronotal angularity, or sinuate (Cryptophagini), or unmodified (Caenoscelini and most Cryptosomatulini); basal pits present (most Cryptophagini) or absent (Caenoscelini and Cryptosomatulini). Hypomeron with notch above procoxal cavity (absent in some Cryptosomatulini and *Asternodea*). Procoxal cavity internally closed, externally open. Prosternum with star-like glandular ducts present (in *Caenoscelis*, some Cryptophagini, and Cryptosomatulini). Mesepimeron with distinct pit (absent among some Cryptosomatulini and Cryptophagini). Meso-metasternal articulation with double knob (absent in some Cryptophagini and Cryptosomatulini). Width of mesosternal process equal to that of mesocoxa in most species. Metasternum with longitudinal line present (most Cryptophagini) or absent (most Cryptosomatulini). Metasubcoxal lines absent (Cryptophagini and most Cryptosomatulini) or present (most Caenoscelini). Spiracles on abdominal segments 6 and 7 present (except for some Cryptophagini). Wing with basal binding patch well developed. Tibia parallel-sided (Cryptophagini) or clubbed (Caenoscelini and most Cryptosomatulini), apical spines present (absent in *Striatocryptus*).

Male.— Aedeagus with arms of tegmen narrowly fused or separate apically (broadly fused in *Striatocryptus*); articulated parameres present. Tarsal formula 554 (555 in some Cryptophagini).

Discussion.— In this revision I recognize 33 genera placed among three tribes in Cryptophaginae.

TRIBE CRYPTOPHAGINI

Cryptophagini Kirby, 1837:vii. Type genus: *Cryptophagus* Herbst 1792.
Telmatophilides Jaquelin du Val, 1859:209. Type genus: *Telmatophilus* Heer 1841.
Antherophagi LeConte, 1861:98. Type genus: *Antherophagus* Latreille, 1829.
Paramecosomina Reitter, 1875:4. Type genus: *Paramecosoma* Curtis, 1833.
Spaniophaeni Casey, 1900:86. Type genus *Spaniophaenus* Reitter, 1875.
Emphyli Casey, 1900:86. Type genus: *Emphylus* Erichson, 1848.

Diagnosis— Conspicuous glandular ducts present in body; microtubules absent. Mandible without serrations on incisor lobe. Width of labial palpomere 1 equal to that of palpomere 2. Without boss on front of head. Gular sutures present. Pronotum with lateral margin serrate or with angularity, basal pits present (absent in some species). Ventrite 5 without thickened setae or pegs. Orientation of aedeagus in body vertical (horizontal in some species). Tibia parallel-sided.

Description.—Conspicuous glandular ducts present in body; microtubules absent. Head without a marginal ridge surrounding antennal concavity; width of palpomere 1 subequal to that of palpomere 2; subgenal spine present (absent in *Paramecosoma, Striatocryptus, Serratomaria, Mnioticus, Telmatophilus,* some *Cryptophagus,* and some *Micrambe*); gular sutures present (absent in *Catopochrotus* and *Asternodea*). Cephalic glandular ducts ending on outside of antennal insertion present in some species. Pronotum with lateral margin serrate or angularity; basal pits present (absent in *Spavius, Spaniophaenus,* some *Cryptophagus, Paramecosoma,* and *Mnionomidius*). Hypomeron with notch present above procoxal cavity (absent in *Asternodea*). Procoxal cavity internally closed; externally open. Metasubcoxal lines absent. Lateral abdominal glandular ducts present on ventrites 1 - 4 (absent in *Pteryngium*). Ventrite 5 without modified setae or pegs. Abdominal spiracles absent or present on segments 6 and 7; spiracle on 7 not modified. Prescutal microsculpture variolate (elongate variolate in *Asternodea*). Hind wing present or absent. Tibia parallel-sided.

Male.— Orientation of aedeagus in body vertical (horizontal in some *Henoticus* and *Mnionomidius*). Tarsal formula 554 (555 in *Mnioticus, Telmatophilus,* and some *Cryptophagus*).

Discussion.— I recognize 20 genera of Cryptophagini. The genus *Fratrhenoticus* Bruce is probably based on a species of the genus *Henoticus*, and is not treated in this paper (see previous discussion).

Genus *Antherophagus* Dejean
(Figs. 34, 119, 174, 175)

Antherophagus Dejean, 1821:45. Type species: *Tenebrio pallens* Linnaeus, 1781, by subsequent designation of Westwood (1840:13).

Diagnosis.—Body form parallel-sided, not strongly compressed. Clypeus of male notched. Antenna clubbed. Pronotum with anterior margin straight; lateral margin simple; angularity present but poorly developed; 1 lateral glandular duct present. Hypomeron without field of pores. Prosternum with star-shaped glandular pores; prosternal process not vaulted. Ventrite 1 longer than remaining ventrites. Tarsal formula 554 in male.

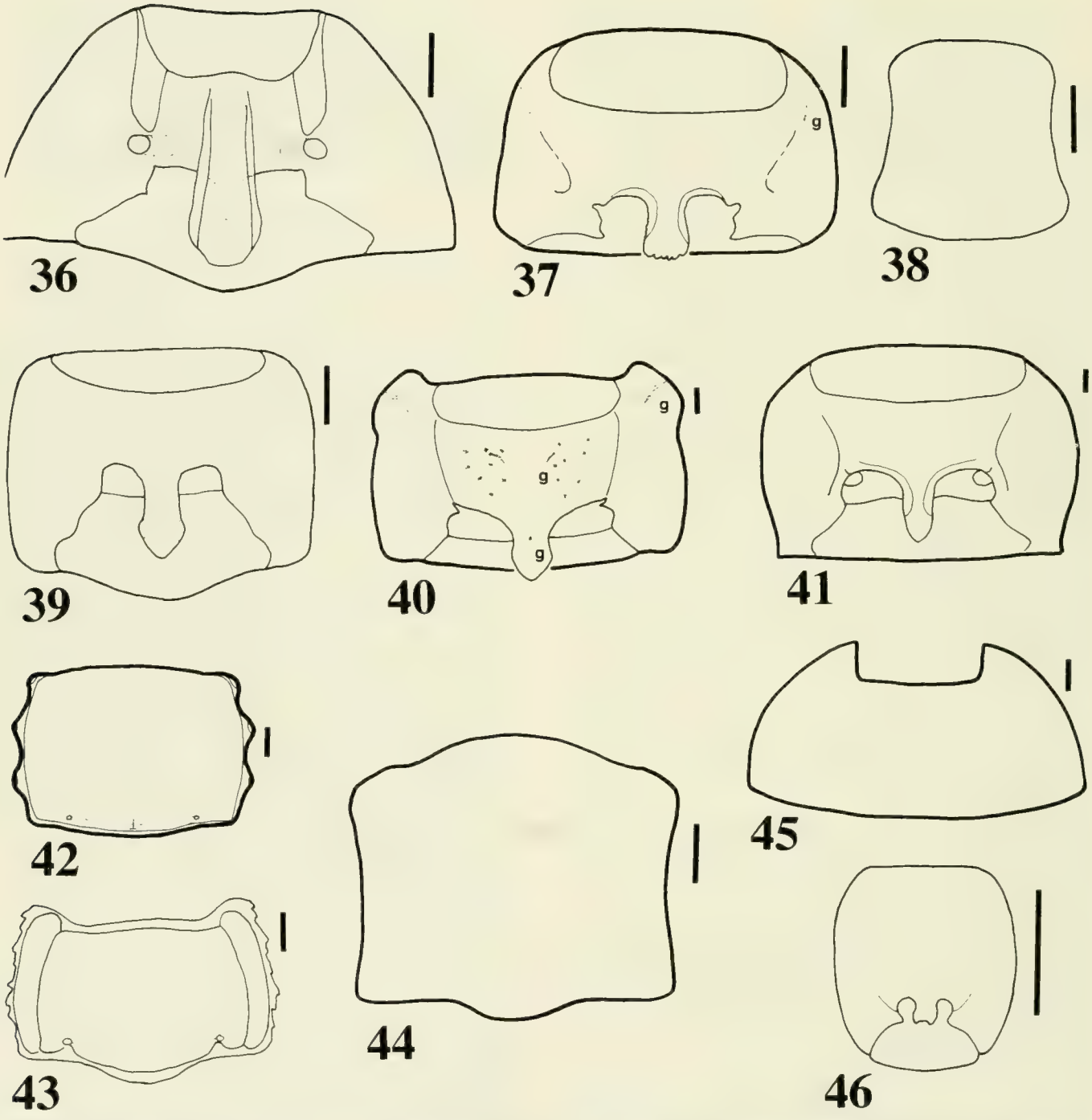
Description.— Length 3.0-5.2 mm. Color of body golden, brown or red brown; mouthparts, flagellum, bases of tibiae dark brown. Body parallel-sided and convex. Body setae short or moderately long, apressed. Punctation of body and elytron confused, punctures present on prosternum. Glandular ducts not saccular. Head with line on the vertex; frontoclypeal suture absent; subgenal spine poorly developed or absent; gular sutures present; cephalic glandular ducts absent. Antenna clubbed; antennomeres slightly compact; last antennomere asymmetrical and subequal in length to penultimate. Mandible without dorsal tubercles. Mentum with a transverse line or ridge. Eye well developed or reduced in some species; ocular setae present. Pronotum parallel-sided with greatest width at middle; anterior margin of pronotum straight; sides not explanate; margin unmodified; middle tooth absent; pronotal angularity present but poorly developed; sublateral line absent; basal pronotal pits present, not connected by groove; median fold absent. Hypomeron with a notch near the procoxal cavity; field of pores absent. Prosternal process not vaulted, glandular duct present. Anterior region of prosternum with or without glandular ducts. Lateral margin of pronotum with 1 glandular duct. Mesepimeron with pit; ringlike cuticle absent. Mesosternum without parallel lines; width of mesosternal process 2/3 that of mesocoxa. Double knob articulation of the meso- and metasternum present. Metasternum with median longitudinal line; pit below coxa present or absent; submesocoxal glandular duct present or absent; discal glandular duct absent. Metendosternite with anterior tendons approximate. Ventrite 1 longer than remaining ventrites; 1 discal glandular duct present or absent. Ventrites with 2 lateral glandular ducts on each side. Abdominal spiracles on segments 1-7. Prescutum with variolate microsculpture. Hind wing present or absent, cell absent, all veins present. Tibia with apical fringe of spines. Tarsomeres slightly lobed below.

Male.— Clypeus notched. Antennal segments compact. Anterior portion of prosternum with star-like glandular ducts. Aedeagal orientation in body vertical; tegmen with anterior arms narrowly fused at distal ends. Ventrite 5 unmodified. Metatibia unmodified. Tarsal formula 554; tarsomeres 1-3 of pro- and mesotarsi dilated.

Diet.— Pollen, debris in *Bombus* nests (Donisthorpe 1920, personal observation).

Habitat.— *Bombus* nests, on flowers (see Chavarria 1994a,b).

Larval descriptions.— *Antherophagus silaceus* Herbst (= *nigricornis*) (Perris 1877); *A. ludekingi* (Mohr and Lieftink 1947); *A. pallens* (Fabricius) (Verhoeff 1923); *Antherophagus* spp. (Böving and Craighead 1931; Lawrence 1991).



Figs. 36-46. Pronota of Cryptophagidae. **36,** *Himascelis* sp. (Nepal), ventral view. **37,** *Chilatomaria australis*, ventral view. **38,** *Cryptafricus leleupi*, dorsal view. **39,** *Neopicrotus peckorum*, ventral view. **40,** *Spavius glaber*, ventral view of male. **41,** *Mnioticus hancocki*, ventral view of male. **42,** *Salebius octodentatus*, dorsal view (drawn after Bousquet 1991). **43,** *Henotiderus obesulum*, dorsal view (drawn after Bousquet 1991). **44,** *Micrambina helmsi*, dorsal view. **45,** *Catopochrotus crematogastri*, dorsal view. **46,** *Amydropa anophthalma*, dorsal view. (Scale bars = 0.1 mm, g = glandular duct).

Distribution.— Holarctic, Southeast Asia, South America.

Discussion.— This genus is composed of 13 described species and I have examined undescribed species from Neotropical regions and Southeast Asia. Major revisions include Casey (1900) for North America and Lohse (1967) for the middle European species. I agree with Bousquet's (1989) suggestion that a revision of the North American species is necessary for establishing limits of species because many of the forms described by Casey (1900) appear similar.

Antherophagus is monophyletic based mainly on behavioral and male secondary sexual characteristics. It is consistently placed in the phylogenetic trees near *Micrambe* and other members of the group.

Asternodea Leschen, new genus
(Figs. 21, 51, 64, 74, 89, 100, 118, 177)

Type species: *Asternodea loebli* Leschen, new species

Diagnosis.—Body form parallel-sided, moderately convex. Antenna clubbed. Clypeus of male not notched. Pronotum with anterior margin straight; lateral margin evenly serrate, not explanate or sinuate; angularity absent; middle tooth absent; sublateral line absent; 1 lateral glandular duct present. Hypomeron without field of pores. Prosternum without star-shaped glandular pores; prosternal process vaulted. Ventrite 1 longer than remaining ventrites. Tarsal formula 554 in male.

Description.— Length 1.2 mm. Color of body brown. Body form parallel-sided, moderately convex. Body setae moderately elongate, decumbent. Punctation of body and elytron confused, punctures present on prosternum. Glandular ducts of body saccular. Head with line on the vertex; frontoclypeal suture absent; subgenal spine present; gular sutures absent; cephalic glandular ducts present. Antenna clubbed, antennomeres not compact; terminal antennomere asymmetrical, subequal in length to penultimate antennomere. Mandible with 2 dorsal tubercles. Mentum with a transverse line or ridge. Eye well developed; ocular setae absent. Pronotum with sides converging anteriorly, greatest width at base; anterior margin of pronotum straight; sides not explanate; pronotal margin evenly serrate, prominent middle tooth absent; pronotal angularity absent; sublateral line absent; basal pronotal pits present, not connected by groove; median fold absent. Hypomeron without notch near procoxal cavity; field of pores absent. Prosternal process vaulted; glandular duct present. Anterior region of prosternum without glandular ducts. Lateral pronotal margin with 1 glandular duct. Mesepimeron with pit; ringlike cuticle present. Mesosternum with parallel lines; width of mesosternal process greater than that of mesocoxa. Double knob articulation of meso- and metasternum absent. Metasternum without median longitudinal line; pit below coxa present; submesocoxal glandular duct absent; discal glandular duct absent. Metendosternite with anterior tendons approximate. Ventrite 1 longer than remaining ventrites; 2 discal glandular ducts present. Ventrites with 2 lateral glandular ducts on each side. Abdominal spiracles absent on segments 6 and 7. Prescutum with elongate variolate microsculpture. Hind wing present; cell formed by a merging of CuA_2 and CuA_{3+4}+AA_{1+2} present; vein MP_3 absent. Tibia with apical fringe of spines. Tarsomeres slightly lobed below.

Male.— Clypeus not notched. Antennal segments not compact. Anterior portion of prosternum without star-like glandular ducts. Aedeagal orientation in body vertical; tegmen with anterior arms narrowly fused at distal ends. Ventrite 5 unmodified. Orientation of aedeagus vertical; tegmen with anterior arms narrowly fused at the distal ends. Metatibia unmodified. Tarsal formula 554; tarsomeres 1-3 of pro- and mesotarsi dilated.

Diet.— Fungal spores and hyphae (personal observation).

Habitat.— Leaf litter.

Distribution.— Nepal.

Discussion.— The genus *Asternodea* is known from a single species which is described below. Its unique appearance, similar in form to members of Caenoscelini, is unusual among Cryptophagini. *Asternodea* is a member of a cluster of genera (*Serratomaria* and *Striatocryptus*) that contain many species with saccular glandular ducts in the body.

Etymology.— The generic name is derived from the root word *Sternodea*, a genus of Caenoscelini that the type species closely resembles, and the Greek prefix a-, meaning not.

Asternodea loebli Leschen, new species
(Figs. 21, 51, 64, 74, 89, 100, 118, 177)

Description.— Length 1.20 mm (n = 2). Color of body brown; elytron infuscate with dark brown margin; mouthparts and legs light brown. Punctation dense, average width of puncture 0.001 mm. Body setae decumbent, arising from slits; average length 0.005 mm. Head densely punctate, punctures separated by about 1/3 diameter; interantennal distance = 0.019 mm. Eye prominent, coarsely faceted. Antenna elongate, extending to basal 1/3 of pronotum; antennomere relative lengths 6:5.5:4:3:3:3:3:3:4:5:7. Pronotum about 0.55 x as long as wide (PL/MPW = 0.55 - 0.56 , x = 0.55); depth = .28 - 0.34, x = 0.31 mm. Lateral margin of pronotum with four evenly spaced teeth at side; punctures of disk separated by about 2/3 punctural width. Prosternal process equal in length to anterior portion of prosternum; width gradually expanding posteriorly; posterior margin flat. Elytra about 1.22 x as long as wide (EL/MEW = 1.21 - 1.24, x = 1.22) and 2.75 x as long as pronotum (EL/PL = 2.63 - 2.86, x = 2.75); punctures separated by 1 diameter. Mesepimeron with a deep pit containing several setae. Metasternal process evenly arcuate. Aedeagus as in Fig. 118.

Discussion.— As the only member of the genus *Asternodea, A. loebli* can be identified by characters in the key to the genera and in the diagnosis of the genus.

Etymology.— Named in honor of I. Löbl, an authority on small beetles, a good friend, and collector of the type species.

Type.—Holotype, male, with labels as follows: "E. Nepal: Kosi. Foret S. Mangsingma 2250 m, 12.IV.84. Löbl - Smetana, HOLOTYPE, *Asternodea loebli* R. Leschen 1994" (MHNG).

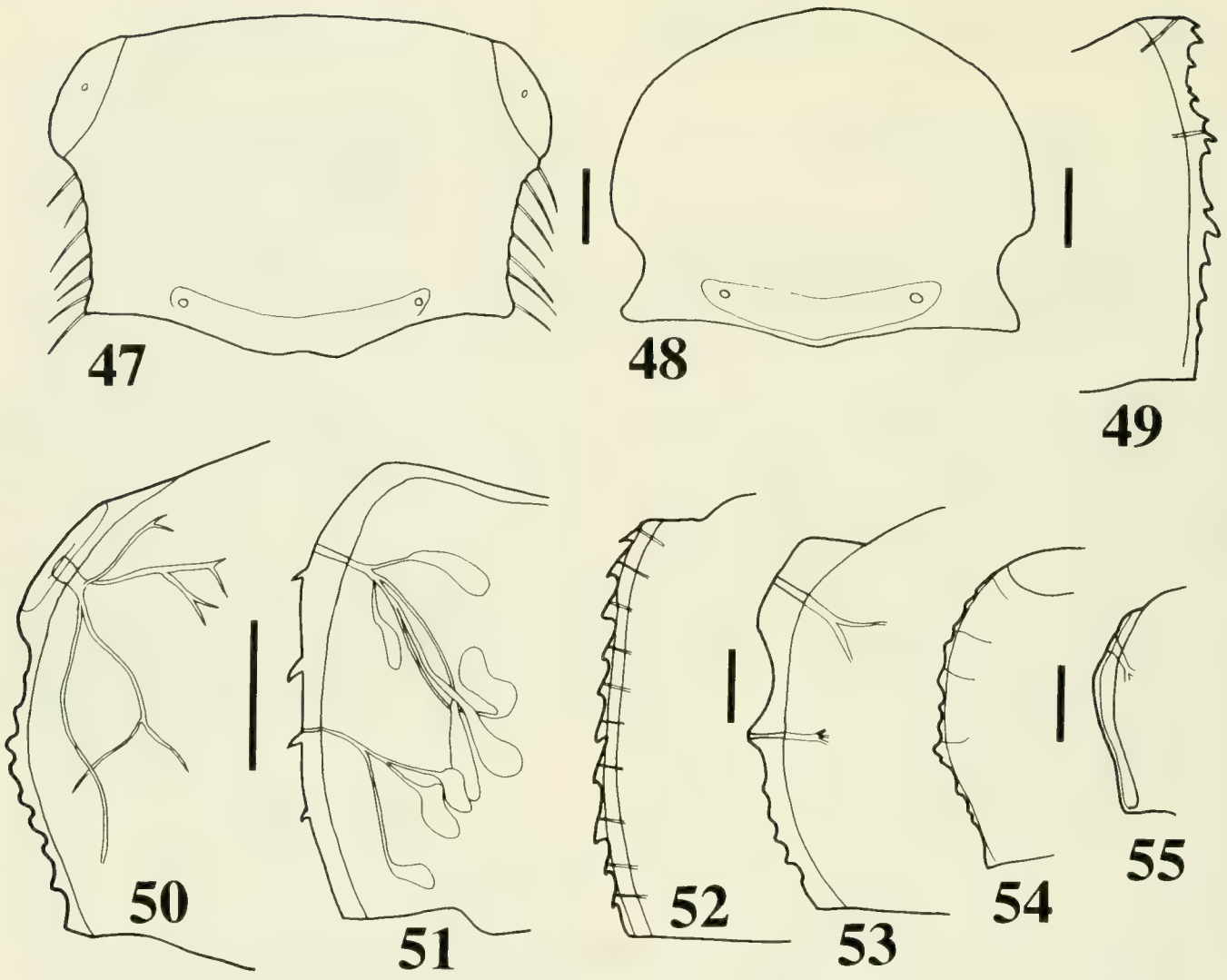
Paratypes.— 3. NEPAL: 1, same data as holotype except Val. Induwa Kola, 2000 m, 18.VI.84 (RALC, on microslide); 1, (Prov. Bagmati), Dobate Ridge NE Barahbise, 2800m, 2.V.81, Löbl & Smetana (MHNG); 1, Khandbari District., For. NE Kuwapani, 2450m, 13.IV.82 A. & Z. Smetana (MHNG, on microslide).

Genus *Catopochrotus* Reitter
(Figs. 33, 45, 178, 179)

Catopochrotus Reitter, 1889:290. Type species: *Catopochrotus crematogastri* Reitter, 1889, by monotypy.

Diagnosis.—Body form limuloid, moderately flattened. Clypeus of male not notched. Antenna clavate. Pronotum with anterior margin emarginate; lateral margin simple; middle tooth absent; not explanate or sinuate; angularity present but poorly developed; sublateral line absent; 1 lateral glandular duct present. Hypomeron without field of pores. Prosternum with star-shaped glandular pores on male; prosternal process vaulted. Ventrite 1 longer than remaining ventrites. Tarsal formula 554 in male.

Description.— Length 2.7 - 3.0 mm. Color of body dark brown. Body form limuloid, moderately flattened. Body setae elongate, apressed. Punctation of body and elytron confused; punctures present on prosternum. Glandular ducts of body not saccular. Head without line on vertex; frontoclypeal suture absent; subgenal spine well developed; gular sutures absent; cephalic glandular ducts absent. Antenna clavate; antennomeres compact; terminal antennomere flattened and symmetrical, subequal in length to that of penultimate. Mandible with 1 dorsal tubercle. Mentum with transverse ridge. Eye well developed, prominent; ocular setae present. Pronotum converging anteriorly with greatest width at base; anterior margin of pronotum emarginate; side not explanate; angularity present, poorly developed; lateral margin unmodified; prominent middle tooth absent; sublateral line absent; basal pits absent; median fold absent. Hypomeron with a notch near the procoxal cavity, field of pores absent. Prosternal process not vaulted, glandular duct present. Anterior region of prosternum without glandular ducts. Lateral margin of pronotum with one glandular duct present. Mesepimeron with pit; ringlike cuticle absent. Mesosternum without parallel lines; width of mesosternal



Figs. 47-55. Pronota of Cryptophagidae. **47,** *Striatocryptus polyglandis*, dorsal view. **48,** *S. wilkinsoni*, dorsal view. **49,** *Henotimorphus belovi*, left side showing glandular ducts. **50,** *Micrambe* sp. (Africa), right side showing glandular ducts. **51,** *Asternodea loebli*, right side showing glandular ducts. **52,** *Mnionomidius serricollis*, right side showing glandular ducts. **53,** *Cryptophagus* sp. (North America), right side showing glandular ducts. **54,** *Neohenoticus palmerae*, right side showing glandular ducts. **55,** *Atomaroides ussurica*, right side showing glandular ducts. (Scale bars = 0.1 mm).

process greater than that of mesocoxa. Double knob articulation of the meso- and metasternum absent. Metasternum with median longitudinal line; pit below coxa absent; submesocoxal glandular duct absent; discal glandular duct absent. Metendosternite with anterior tendons approximate. Ventrite 1 longer than remaining ventrites; 1 discal glandular duct present. Abdomen with 2 lateral glandular ducts present on each side. Abdominal spiracles present on segments 1 - 7. Prescutum with variolate microsculpture. Hind wing present; cell absent; all veins present. Tibia with apical fringe of spines. Tarsomeres slightly lobed.

Male.— Clypeus not notched. Antennal segments not compact. Anterior portion of prosternum with star-like glandular ducts. Aedeagal orientation in body vertical; tegmen with anterior arms narrowly fused at distal ends. Ventrite 5 unmodified. Metatibia unmodified. Tarsal formula 554; tarsomeres not modified.

Diet.— Saprophagous (personal observation).

Habitat.— Ant nests of the genus *Crematogaster* (Reitter 1889, Kistner 1982).

Distribution.— Caucasia.

Discussion.— The genus *Catopochrotus* contains one species, *C. crematogastri*, which is associated with ants and has a limuloid body form that is unique among cryptophagids. Behavioral observations on this species would give clues to the adaptive significance of its body form and level of integration into the nest of its ant host. Because it is fully winged, unlike some members of *Antherophagus*, dispersal to new ant colonies may not require a phoretic association with its host ant.

Catopochrotus is consistently placed in the cladograms as sister taxon to *Spaniophaenus*, another genus that contains species inquilines of social insects.

Genus *Cryptophagus* Herbst
(Figs. 17, 53, 73, 140, 143, 163, 180)

Cryptophagus Herbst, 1792:172. Type species: *Dermestes cellaris* Scopoli,

1763, by subsequent designation (Westwood 1840:13), see notes by Bousquet (1989).

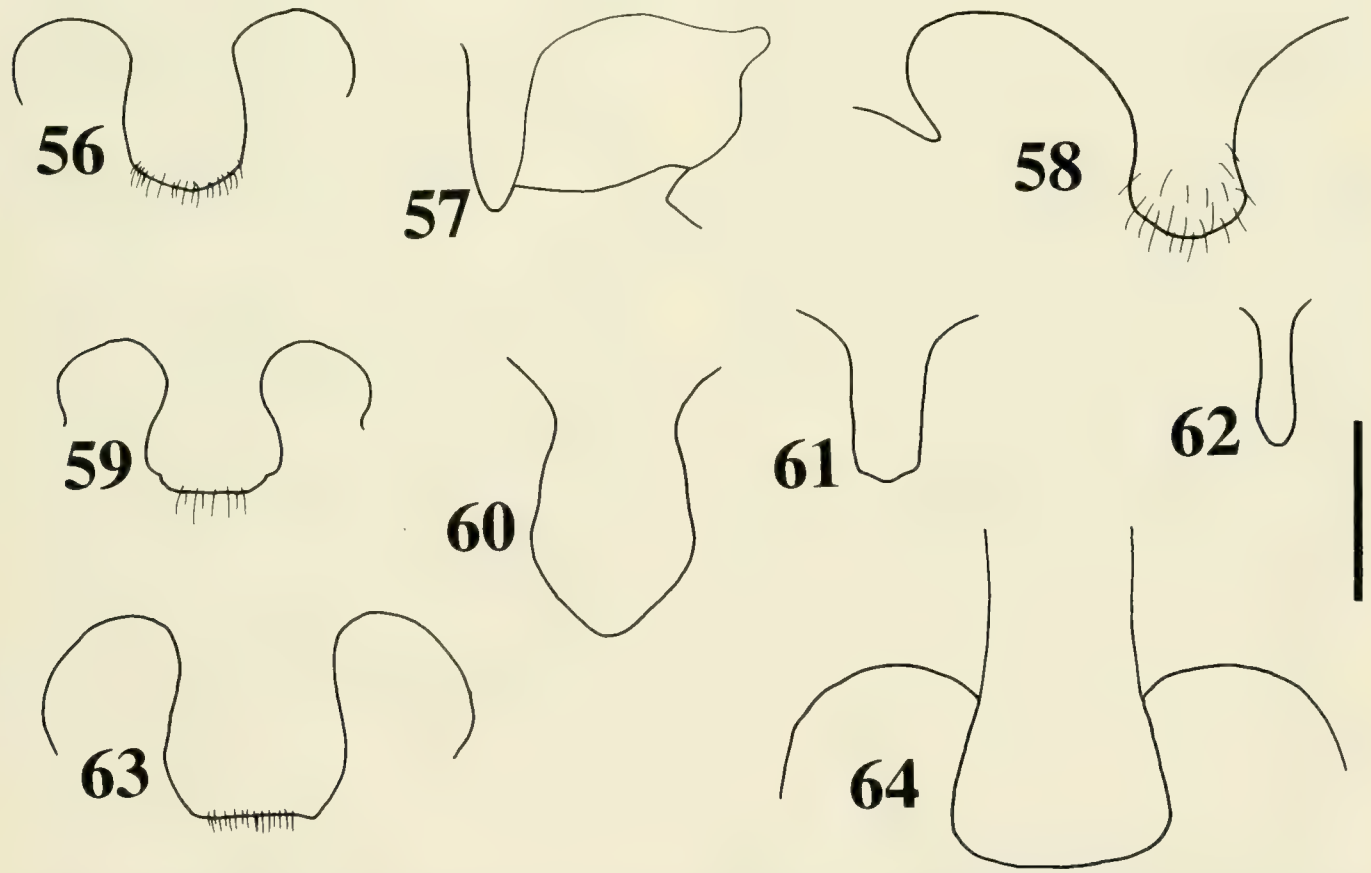
Mniomus Wollaston, 1864:138. Type species: *Mniomus elliptic us* Wollaston, 1864, by monotypy (first synonymized under the name *Cryptophagus* by Coombs and Woodroffe 1962:66).

Cryptophagistes Crotch, 1873:44. Type species: *Dermestes cellaris* Scopoli, 1763, by subsequent designation (Bousquet 1989:6) (first synonymized under the name *Cryptophagus* by Austin 1880:19).

Micrambinus Reitter in Heyden et al., 1906:322. Type species: *Dermestes bimaculatus* Panzer, 1798, here designated (first synonymized under the name *Micrambe* by Bruce 1936:21).

Diagnosis.—Body form parallel-sided, moderately convex. Clypeus of male not notched. Antenna clubbed. Pronotum with anterior margin straight; lateral margin evenly serrate, serrations are reduced or absent in some species; not explanate or sinuate; angularity present, poorly developed in some species; prominent middle tooth present in most species; sublateral line absent; 1-3 lateral glandular ducts present. Hypomeron without field of pores. Prosternum with star-shaped glandular pores on male; prosternal process not vaulted. Ventrite 1 longer than remaining ventrites. Tarsal formula 554 in male (555 in some species).

Description.—Length 2.0-4.2 mm. Color of body variable; brown, red brown, bicolored, black, elytra maculate in some species. Body form parallel-sided, moderately convex. Body setae variable; suberect, apressed, decumbent, biseriate, or uniseriate. Punctation of body and elytron confused. Glandular ducts of body not saccular. Head with line on vertex; frontoclypeal suture absent; subgenal spine present or poorly developed; gular sutures present; cephalic glandular ducts absent. Antenna clubbed, antennomeres not or slightly compact; terminal antennomere asymmetrical, subequal in length to that of penultimate. Mandible with 2 or 3 dorsal tubercles. Mentum with a transverse line or ridge. Eye well developed, reduced in some species; ocular setae present. Pronotum parallel-sided with greatest width at middle; anterior margin of pronotum straight; sides not explanate; margin evenly serrate or unmodified; prominent middle tooth present or absent; pronotal angularity present, sometimes poorly developed; sublateral line absent; basal pits present or not, not connected by a groove; median fold present or absent. Hypomeron with a notch near the procoxal cavity, without field of pores. Prosternal process not vaulted, glandular duct present. Anterior region of prosternum with glandular ducts. Lateral margin of pronotum with 1-3 glandular ducts, not saccular. Mesepimeron with pit; ringlike cuticle absent. Mesosternum without parallel lines, width of mesosternal process equal to or 2/3 that of mesocoxa. Double knob articulation of meso- and metasternum present. Metasternum with median longitudinal line; pit below coxa present; submesocoxal glandular duct present or not. Metendosternite with anterior tendons approximate or widely separate. Ventrite 1 longer than remaining ventrites; discal glandular ducts present or not. Ventrites with 2 lateral glandular ducts on each side. Abdominal spiracles present on segments 1-7. Prescutum with variolate microsculpture. Hind wings present or absent; cell absent; all veins present. Tarsomeres slightly lobed below.



Figs. 56-64. Prosternal processes of Cryptophagidae. **56,** *Paratomaria crowsoni.* **57,** *Cryptafricus leleupi.* **58,** *Cryptogasterus lawrencei.* **59,** *Microatomaria hintoni.* **60,** *Striatocryptus wilkinsoni.* **61,** *Anitamaria thayerorum.* **62,** *Microphagus johnsoni.* **63,** *Chilatomaria hillersae.* **64,** *Asternodea loebli.* (Scale bar = 0.1 mm).

Male.— Clypeus not notched. Antennal segments not compact. Anterior portion of prosternum with star-like glandular ducts. Orientation of aedeagus vertical; tegmen with anterior arms separate or narrowly fused at distal ends. Ventrite 5 unmodified. Metatibia unmodified. Tarsal formula 554 or 555; tarsomeres 1-3 of pro- and mesotarsi dilated.

Diet.— Fungal spores and hyphae (Hinton 1945).

Habitat.— Leaf litter, rotting wood, mammal nests, social insect nests, macrofungi (Falcoz 1929, Hinton 1945, Coombs and Woodroffe 1955, Woodroffe and Coombs 1961, Lawrence 1991).

Larval descriptions.— *Cryptophagus acutangulus* (Hinton and Stephens 1941; Hinton 1945; Klippel 1952); *C. badius* Sturm (Rey 1887; Xembeu 1907); *C. cellaris* (Newport 1850; Verhoeff 1923; Hinton 1945); *C. dentatus* (Perris 1862,1877; Xembeu 1906; Falcoz 1924; Hinton 1945; Klippel 1952); *C. distinguendus* (Xembeu 1907); *C. hirtus* Gyllenhal (Blisson 1847); *C. lycoperdi* (Falcoz 1924); *C. pilosus* Gyllenhal (Erichson 1848); *C. pubescens* (Rey 1887; Falcoz 1924); *C. saginatus* (Rey 1887; Xembeu 1898, 1906; Falcoz 1924; Böving and Craighead 1931; Klippel 1952); *C. scanicus* (Xembeu 1901, 1906; Hinton 1945); *C. subfumatus* Kraatz (Mjöberg 1906; Klippel 1952); *Crytpophagus* spp. (Verhoeff 1923; Peterson 1951; Lawrence 1991).

Distribution.— Holarctic, Africa, worldwide (some pest species).

Discussion.— The genus *Cryptophagus* contains about 200 described species and includes numerous undescribed species from Asia, Central America, and North America. Major revisionary works and keys include the following: Bruce (1936, Europe), Casey (1900, North America), Coombs and Woodroffe (1955, Great Britain), Emetz (1977, Mongolia), Hatch (1962, northwestern North America), Ljubarsky (1992b, Caucasus; 1992c, northeastern Russia), Lohse (1967, middle Europe), Otero (1990, Canary Islands), Rĕska (1994, middle Europe), Woodroffe and Coombs (1961, North America).

Cryptophagus is one of the most taxonomically difficult genera among Cryptophagidae because of the extensive morphological variation existing among its members. Some of this variation can be attributed to shape differences associated with hind wing loss in montane and island forms. There has been confusion among some taxonomists as to the status and limits of *Cryptophagus* and its subgenera. While major issues have been discussed by Bruce (1936, 1952) and Coombs and Woodroffe (1962), many problems still exist and clarification of these requires a detailed cladistic study of the entire genus and its relatives which is beyond the scope of this study. Below I discuss the taxonomic status of subgenera and the confusion about them.

Wollaston (1864) erected the genus *Mnionomus* for a flightless species, *C. ellipticus*, that he described from the Canary Islands. This name was used as a subgenus by Falcoz (1929) and Bruce (1936) while Scott (1935) treated it as a genus. As a subgenus of *Cryptophagus*, *Mnionomus* included those members that lack fully developed hind wings. Subsequently, Coombs and Woodroffe (1962) studied the generic limits of *Mnionomus* and *Cryptophagus*, and despite previous attempts at defining these as separate taxa (e.g., Dajoz 1959), they concluded that these "form a graded series linking the extreme form, *ellipticus*, with *Cryptophagus* sens. str. and that no clear distinction can be drawn between them, even at subgeneric level"(p. 63). In this work, Coombs and Woodroffe (1962) examined the African species described by Scott (1935) and assigned them to the correct genera.

Despite the previous confusion as to the placement of species in either *Micrambe* or *Cryptophagus* by some authors, Bruce (1936, see also 1952) and most European workers as noted above considered *Micrambe* as a subgenus of *Cryptophagus*. These genera have been treated separately however in recent works (e.g., Coombs and Woodroffe 1962, Johnson 1992, Rĕska 1994). Based on cladistic analysis, *Micrambe* is separate from *Cryptophagus* and is consistently placed in a basal position in the *Cryptophagus* group in the cladograms. Because Bruce recognized *Micrambe* as a subgenus of *Cryptophagus*, all the species described by him in the subgenus *Micrambe* must be formally transferred to the genus *Micrambe*. New combinations resulting from this action are noted in the Appendix for taxa whose types I have examined.

The subgenus *Micrambinus* Reitter was proposed for several species of *Cryptophagus* (Reitter 1906). Later *Micrambinus* was placed in *Micrambe* by Bruce (1936) who considered it as a subgenus of *Cryptophagus*. Certain species that I have examined (such as *Cryptophagus micramboides* and some undescribed forms) from the eastern Palaearctic appear similar to the European species *C. bimaculatus*. These do not have a prominent middle tooth on the lateral margin of the pronotum and the serrations terminate proximal to the angularity (in *Micrambe* the serrations are present from the middle of the prothorax to the posterior angle). Although these appear similar to *Micrambe*, I have placed these in *Cryptophagus* because they have star-shaped prosternal glandular ducts in the male and there are two lateral pronotal glandular ducts instead of one as in *Micrambe*.

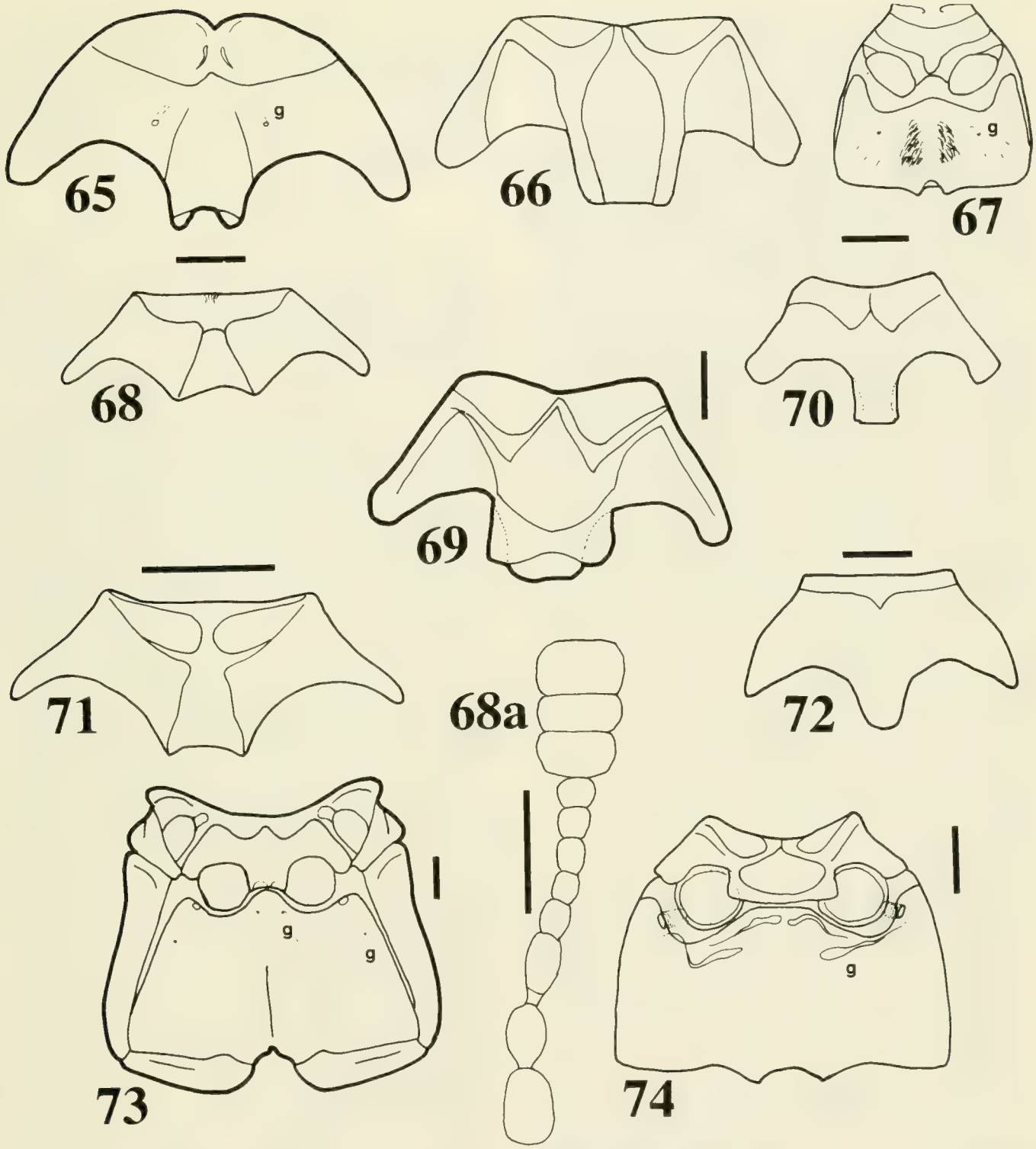
The genus *Myrmedophila* was described by Bousquet (1989) for the single American species *M. americana* (LeConte) which is an inquiline in *Formica* ant nests. This genus appears similar in form to members of the European genus *Spavius*, which also occurs in *Formica* nests. On the other hand, *Myrmedophila* also appears similar to many species of *Cryptophagus*, and Ljubarsky (1992d) has placed *Myrmedophila* as a subgenus of *Cryptophagus*. Based on my cladistic analysis, *Myrmedophila* is outside of *Cryptophagus*, although when behavioral characters are eliminated from the cladistic analysis, *Myrmedophila*, *Cryptophagus*, and other genera collapse into a polytomy. The formation of this polytomy suggests that perhaps Ljubarsky is correct in his taxonomic conclusion, but that the recognition of several other genera may create a paraphyletic grouping of his *Cryptophagus*. In this study I have retained the genus *Myrmedophila*.

Also included in the genus *Cryptophagus* are the species *C. enormis* Hisamatsu and *C. maximus* Blake with similar forms and habits; both species occur in the pouch fungus *Cryptoporus* and have the prominent middle tooth of the pronotum modified into an "angularity". The similarity of these forms to *Salebius*, which has the pronotal margins produced into three lobes that are similar in form to angularities, lead Bousquet (1989) to the possibility that *Salebius* may be a subgenus of *Cryptophagus*. An unusual undescribed species from Oaxaca, Mexico has two distinct lateral teeth, a distinct angularity, and three glandular ducts associated with these on the pronotum. More firm taxonomic conclusions would require a fine-grained study of the *Cryptophagus*-group, including more terminal taxa to better represent the total variation of *Cryptophagus*.

As stated above, there is the possibility that *Cryptophagus* represents a paraphyletic grouping of unrelated taxa. This is also indicated by the lack of a single unique synapomorphy for members of *Cryptophagus*. In my cladistic analysis I was concerned mainly with the taxonomic distinction between *Micrambe* and *Cryptophagus* and the relationships among other genera of Cryptophagidae. The apparent resolution of this group in my analysis may be an artifact because I treated members of the genus *Cryptophagus* superficially.

Genus *Henoticus* Thomson
(Fig. 181)

Henoticus Thomson, 1868:67. Type species: *Cryptophagus serratus* Gyllenhal, 1868, by subsequent designation (Bollow 1941:570).



Figs. 65-74. Morphological features of Cryptophagidae. **65,** *Chilatomaria australis*, mesosternum. **66,** *Neopicrotus peckorum*, mesosternum. **67,** *Microphagus johnsoni*, meso- and metasternum. **68,** *Cryptogasterus lawrencei*, mesosternum. **68a,** same, antenna. **69,** *Serratomaria vulgaris*, mesosternum. **70,** *Striatocryptus wilkinsoni*, mesosternum. **71,** *Anitamaria thayerorum*, mesosternum. **72,** *Cryptafricus leleupi*, mesosternum. **73,** *Cryptophagus* sp., meso- and metasternum (after Bousquet 1991). **74,** *Asternodea loebli*, mesosternum. (Scale bars = 0.1 mm, g = glandular duct).

Contophthalma Kangas, 1963:70. Type species: *Henoticus germanicus* Reitter, 1906 (= *Cryptophagus californicus* Mannerheim 1843), by original designation (first synonymized under the name *Henoticus* by Hinton 1945:203).

Glyptophorus Park, 1929:430. Type species: *Glyptophorus mycetoecus* Park, 1929, by monotypy (first synonymized under the name *Henoticus* by Bousquet 1989:12).

Diagnosis.—Body form parallel-sided, moderately convex. Clypeus of male not notched. Antenna clubbed. Pronotum with anterior margin straight; lateral margin evenly serrate, not explanate or sinuate; angularity absent; prominent middle tooth absent; sublateral line absent; glandular ducts absent. Hypomeron with field of pores in both sexes. Anterior portion of prosternum without star-shaped glandular pores; prosternal process not vaulted. First ventrite longer than remaining ventrites. Tarsal formula 554 in male.

Description.— Length 1.2-2.5 mm. Color of body light, dark, or red brown, bicolored, elytra are maculate in some species. Body form parallel-sided, moderately convex. Body setae erect, suberect, apressed, or decumbent, some wingless forms are asetose. Punctation of body and elytron confused. Glandular ducts of body not saccular. Head with line on vertex; frontoclypeal suture absent; subgenal spine present; gular sutures present; cephalic glandular ducts present. Antenna clubbed, antennomeres not compact; terminal antennomere asymmetrical and subequal in length to that of penultimate antennomere. Mandible with two dorsal tubercles. Mentum with a transverse line or ridge. Eye well developed, typically prominent; ocular setae present. Pronotum parallel-sided with greatest width at middle; anterior margin straight; side not explanate; margin evenly serrate; pronotal angularity absent; prominent middle tooth absent; sublateral line absent; basal pits present, connected by a groove; median fold absent. Lateral margin of pronotum without glandular ducts. Hypomeron with a notch near the procoxal cavity; field of pores present. Prosternal process not vaulted; glandular duct present. Anterior region of prosternum without star-shaped glandular ducts. Mesepimeron with pit; ringlike cuticle absent. Mesosternum without parallel lines; width of mesosternal process equal to that of mesocoxa. Double knob articulation of meso- and metasternum present. Metasternum with median longitudinal line; pit below coxa present; submesocoxal glandular duct absent; discal glandular duct present. Metendosternite with anterior tendons approximate or widely separate. Ventrite 1 longer than remaining ventrites; discal glandular duct absent. Ventrites with 2 lateral glandular ducts on each side. Abdominal spiracle absent from segment 7. Prescutum with variolate microsculpture. Hind wings present or absent; cell absent; vein MP3 absent. Tibia with apical fringe of spines. Tarsomeres slightly lobed below.

Male.— Clypeus not notched. Antennal segments not compact. Anterior portion of prosternum without star-like glandular ducts. Orientation of aedeagus vertical or horizontal in body; tegmen with anterior arms separate or fused narrowly at distal ends. Ventrite 5 unmodified. Metatibia unmodified. Tarsal formula 554 or 555; tarsomeres 1-3 of pro- and mesotarsi dilated.

Diet.— Fungal spores and hyphae (Hinton 1945, personal observation).

Habitat.— Leaf litter, rotting wood, stored products, male cycads (Hinton 1945, personal observation).

Larval descriptions.— *Henoticus californicus* (Falcoz 1922; Böving and Craighead 1931; Hinton 1945).

Distribution.— Holarctic, Afrotropical, Neotropical, Australia (undescribed form), worldwide (some pest species).

Discussion.— The genus *Henoticus* contains 32 species, and there are undescribed forms in Africa and Central America. The fauna of India has been reviewed by Johnson (1975a) and Sen Gupta and Pal (1980). Based on the original description, the genus *Fratrhenoticus* Bruce (1963) is probably a species of *Henoticus* with a 2-segmented antennal club.

Henoticus is a distinct monophyletic genus (based on a unique combination of characters); however, its wingless members with reduced serrations may be confused with those of *Mnioticus* where both genera are sympatric in montane east Africa. *Henoticus* can be distinguished from *Mnioticus* by the lack of pronotal lateral glandular ducts and ventrite 1 which is longer than remaining ventrites in the former.

The genus *Henoticus* is related to members of an informal group of cryptophagines that lack a pronotal angularity called the *Henoticus* group.

Genus *Henotiderus* Reitter
(Figs. 43, 127, 139, 142, 145, 176)

Henotiderus Reitter, 1877a:25. Type species: *Henotiderus centromaculatus* Reitter, by monotypy.

Crosimus Casey, 1900:89. Type species: *Crosimus obesulus* Casey, 1900, by subsequent designation (Bousquet 1989:10; first synonymized under the name *Henotiderus* by Bousquet 1989:10)

Henoticoides Hatch, 1962:217. Type species: *Henoticoides lorna* Hatch, 1962, by monotypy (first synonymized under the name *Henotiderus* by Bousquet 1989:10).

Diagnosis.—Body form parallel-sided, moderately convex. Clypeus of male not notched. Antenna clubbed. Pronotum with anterior margin emarginate; lateral margin irregularly serrate, not explanate or sinuate; angularity absent; prominent middle tooth absent; sublateral line present; 3 lateral glandular ducts present. Hypomeron with field of pores. Prosternum without star-shaped glandular pores; prosternal process not vaulted. Ventrite 1 longer than remaining ventrites. Tarsal formula 554 in male.

Description.— Length 1.7-2.3 mm. Color of body light, dark, red brown, bicolored, elytra maculate in one species. Body form parallel-sided, moderately convex. Body setae biseriate, erect, decumbent. Punctation of body confused; elytra striate (not in one undescribed species), each stria 2 punctures wide. Glandular ducts of body nor saccular. Head with line on vertex; frontoclypeal suture absent; subgenal spine well developed; gular sutures present, cephalic glandular ducts present. Antenna clubbed; antennomeres slightly compact; last antennomere asymmetrical and subequal in length to that of penultimate. Mandible with 3 dorsal tubercles. Mentum without transverse line or ridge. Eye well developed, protuberant; ocular setae absent. Pronotum parallel-sided with greatest width at middle; anterior margin emarginate; sides not explanate; margin irregularly serrate; angularity absent; prominent middle tooth absent; sublateral line present; basal pits present, connected by groove; median fold absent. Lateral margin with 3 glandular ducts. Hypomeron with a notch near the procoxal cavity. Prosternal process not vaulted, glandular duct present. Anterior region of prosternum with glandular ducts. Mesepimeron with pit; ringlike cuticle present. Mesosternum without parallel lines; width of mesosternal process equal to that of mesocoxa. Double knob articulation of meso- and metasternum absent. Metasternum with median longitudinal line; pit below coxa present; submesocoxal glandular duct present; discal glandular duct present. Metendosternite with anterior tendons approximate. Ventrite 1 equal to remaining ventrites; 1 discal glandular duct present. Ventrites with 2 lateral glandular ducts on each side. Abdominal spiracle absent from segment 7. Prescutum with variolate microsculpture. Hind wing present; cell formed by a merging of CuA_2 and CuA_{3+4}+AA_{1+2} present; all veins present. Tibia with apical fringe of spines. Tarsomeres slightly lobed.

Male.— Clypeus not notched. Antennal segments not compact. Hypomeron with a field of pores. Anterior portion of prosternum without star-like glandular ducts. Orientation of aedeagus vertical; tegmen with anterior arms separate or narrowly fused at distal ends. Ventrite 5 unmodified. Metatibia unmodified. Tarsal formula 554; tarsomeres 1-3 of pro- and mesotarsi dilated.

Diet.— Fungal spores and hyphae (personal observation).

Habitat.— Rotting logs, lignicolous fungi (Weiss and West 1920, personal observation).

Distribution.— Holarctic.

Discussion.— The genus *Henotiderus* contains three described species, and there are three undescribed species from western North America and Taiwan. Examination of the type specimens reveals that *H. obesulum* (Casey) and *H. hirtus* (Casey) are the same, **new synonymy**.

Henotiderus is a monophyletic group based on characters of the pronotum and is included in the *Henoticus* group.

Genus *Henotimorphus* Ljubarsky
(Fig. 49)

Henotimorphus Ljubarsky, 1987b:951. Type species: *Henotimorphus belovi* Ljubarsky, 1987, by original designation.

Diagnosis.—Body form parallel-sided, moderately convex. Clypeus of male not notched. Antenna clubbed. Pronotum with anterior margin straight; lateral margin irregularly serrate, not explanate or sinuate; angularity absent; prominent middle tooth absent; sublateral line absent; 2 lateral glandular ducts present. Hypomeron without field of pores. Prosternum with star-shaped glandular pores; prosternal process not vaulted. Ventrite 1 longer than remaining ventrites. Tarsal formula 554 in male.

Description.—Length 2.2 mm. Color of body dark brown. Body parallel-sided, moderately convex. Body setae moderately elongate, erect. Punctation of body and elytron confused. Glandular ducts of body not saccular. Head with line on vertex; frontoclypeal suture absent; subgenal spine poorly developed; gular sutures present; cephalic glandular ducts absent. Antenna clubbed; antennomeres slightly compact; last antennomere asymmetrical and subequal in length to that of penultimate. Mandible without dorsal tubercles. Eye well developed, prominent; ocular setae present. Pronotum parallel-sided with greatest width at middle; anterior margin straight; sides not explanate; margin irregularly serrate; angularity absent; prominent middle tooth absent; sublateral line absent; basal pits present, connected by a groove; median fold absent. Lateral margin of pronotum with 2 glandular ducts, not saccular. Hypomeron with notch near the procoxal cavity; field of pores absent. Prosternal process not vaulted, glandular duct present. Anterior region of prosternum without glandular ducts. Mesepimeron without pit. Mesosternum without parallel lines; width of mesosternal process equal to that of mesocoxa. Double knob of mesometasternal junction present. Metasternum with median longitudinal line; pit below coxa present; submesocoxal glandular duct present; discal glandular duct present. Metendosternite with anterior tendons approximate. Ventrite 1 longer than remaining ventrites; 1 discal glandular duct present. Ventrites with 2 lateral glandular ducts on each side. Abdominal spiracles on segments 1-7. Prescutum with variolate microsculpture. Hind wing present; vein MP_3 absent. Tibia with apical fringe of spines. Tarsomeres slightly lobed below.

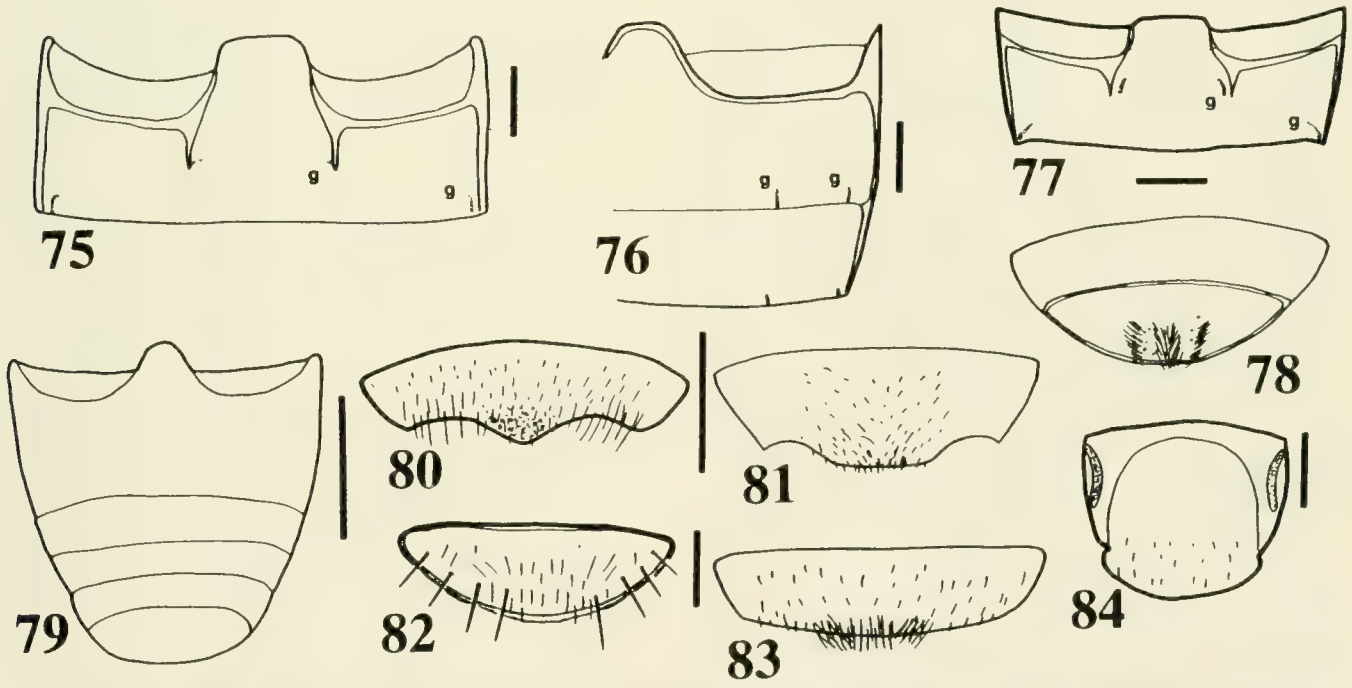
Male.— Clypeus not notched. Antennal segments not compact. Anterior portion of prosternum with star-like glandular ducts. Orientation of aedeagus vertical; tegmen with anterior arms separate or narrowly fused at distal ends. Ventrite 5 unmodified. Metatibia unmodified. Tarsal formula 554; tarsomeres 1-3 of pro- and mesotarsi dilated.

Diet.— Fungal spores and hyphae (personal observation).

Distribution.— Palaearctic.

Discussion.— The genus *Henotimorphus* is monotypic and can be distinguished from other members of Cryptophagini in the form of the pronotum: the lateral pronotal margin has irregularly spaced serrate teeth, the disk lacks a sublateral line, and the glandular ducts are not saccular.

The phylogenetic placement of *Henotimorphus* is at the base of the *Cryptophagus* group in the SAW trees. However, this genus is



Figs. 75-84. Abdominal features of Cryptophagidae. **75,** *Chilatomaria hillersae*, abdominal sternite 1. **76,** *Neohenoticus palmerae*, abdominal sterna 1 and 2. **77,** *Microatomaria hintoni*, abdominal sternite 1. **78,** *Stratocryptus wilkinsoni*, abdominal sterna 4 and 5. **79,** *Neopicrotus peckorum*, abdominal sterna 1-5. **80,** *Antamaria* sp., abdominal sternite 5. **81,** *Microphagus johnsoni*, abdominal sternite 5. **82,** *Brounina* sp. (Chile), abdominal sternite 5. **83,** *Cryptafricus leleupi*, abdominal sternite 5. **84,** *Cryptophagus gibbipennis*, abdominal tergite 7. (Scale bars = 0.1 mm).

often grouped with, and looks more similar to members of the *Henoticus* group in other analyses.

Genus *Micrambe* Thomson
(Figs. 50, 90, 184)

Micrambe Thomson, 1863:263. Type species: *Dermestes abietis* Paykull, 1798, here designated.

Diagnosis.—Body form parallel-sided, moderately convex. Clypeus of male not notched. Antenna clubbed. Pronotum with anterior margin straight; lateral margin evenly serrate (sometimes serrations reduced or absent), not explanate or sinuate; angularity absent; prominent middle tooth absent; sublateral line absent; 1 lateral glandular duct present. Hypomeron without field of pores. Prosternum without star-shaped glandular pores; prosternal process not vaulted. Ventrite 1 longer than remaining ventrites. Tarsal formula 554 in male.

Description.—Length 1.3-3.0 mm. Color light, red, or dark brown, black, or bicolored. Body parallel-sided, moderately convex. Body setae erect, suberect, apressed, or decumbent. Punctation of body and elytron confused. Glandular ducts of body not saccular. Head with line on vertex; frontoclypeal suture absent; subgenal spine present or poorly developed; gular sutures present; cephalic glandular ducts present or absent. Antenna clubbed; antennomeres not compact; last antennomere asymmetrical and subequal in length to that of penultimate. Mandible with 3 dorsal tubercles. Mentum with a transverse line or ridge. Eye well developed, prominent; ocular setae present. Pronotum parallel-sided with greatest width at middle; anterior margin of pronotum straight; sides not explanate; lateral margin evenly serrate; pronotal angularity present; prominent middle tooth absent; sublateral line absent; basal pits present, not connected by a groove; medial fold present or absent. Lateral margin of pronotum with 1 glandular duct. Hypomeron with notch near the procoxal cavity; field of pores absent. Prosternal process not vaulted; glandular duct present. Anterior region of prosternum without glandular ducts. Mesepimeron with or without pit; ringlike cuticle absent. Mesosternum without parallel lines; width of mesosternal process 2/3 or equal to that of mesocoxa. Double knob articulation of meso- and metasternum present. Metasternum with median longitudinal line; pit below coxa present or absent; submesocoxal glandular duct present or absent; discal glandular duct absent. Metendosternite with anterior tendons of metendosternite approximate, widely spaced, or absent. Ventrite 1 longer than remaining ventrites; discal gland absent or present. Ventrites with 2 lateral glandular ducts on each side. Abdominal spiracles on segments 1-7. Prescutum with variolate microsculpture. Hind wings present or absent; cell absent; all veins present or MP_3 absent. Tibia with apical fringe of spines. Tarsomeres slightly or not lobed.

Male.— Clypeus not notched. Antennal segments not compact. Anterior portion of prosternum without star-like glandular ducts. Orientation of aedeagus vertical; tegmen with anterior arms separate or narrowly fused at distal ends. Ventrite 5 unmodified. Metatibia unmodified. Tarsal formula 554; tarsomeres 1-3 of pro- and mesotarsi dilated.

Diet.— Fungal spores and hyphae (Falcoz 1929, personal observation).

Habitat.— Decaying flowers, caterpillar nests, leaf litter, rotting logs (Falcoz 1929, Scott 1935, Coombs and Woodroffe 1955).

Distribution.— Europe, Africa, and Asia.

Discussion.— The genus *Micrambe* contains about 80 described species. Major revisionary works and keys have been made by Bruce (1936, Europe), Coombs and Woodroffe (1955, Great Britain), Otero (1990, Canary Islands), Lohse (1967) and Rĕska (1994) (both middle Europe).

Micrambe has been treated either as a genus or as a subgenus of *Cryptophagus* (see discussion under *Cryptophagus*). Coombs and Woodroffe (1962) assigned some of the African species described by Scott (1935), once included in *Mnionomus*, to *Micrambe*.

Examination of the holotype of *Pteryngium duclouxi* Grouvelle from China reveals that it is a member of *Micrambe*, based on the structure of the pronotum. Therefore, this species is transferred to *Micrambe*.

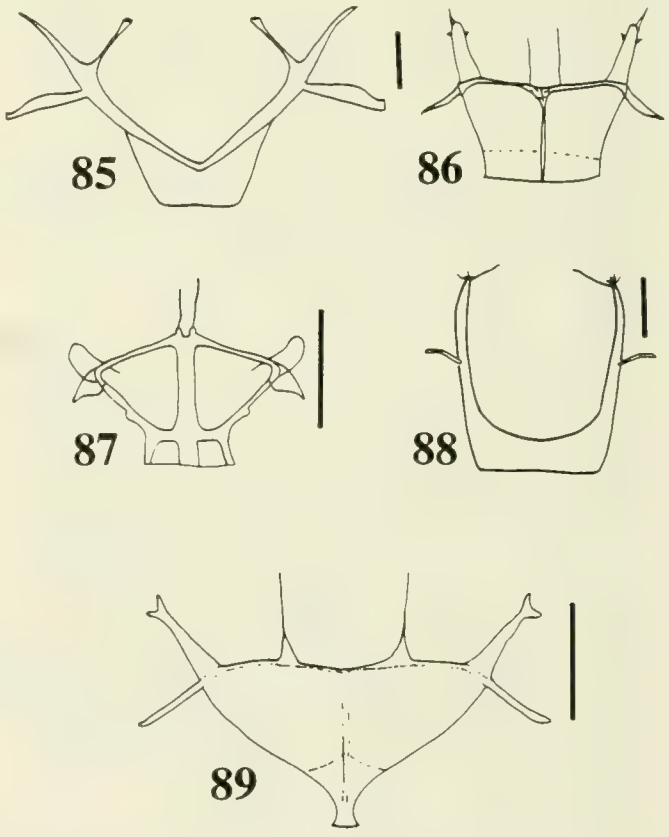
The African fauna is particularly rich in species of *Micrambe* and contains two groups of taxa: One group has species that are brachypterous, bicolored or uniformly dark in color, and are limited to montane east Africa. The other group contains species that are generally light brown in color, have body setae that arise from slits, and are not limited to montane areas of east Africa.

The genus *Micrambe* is a member of the *Cryptophagus* group.

Genus *Mnionomidius* Reitter
(Figs. 52, 183)

Mnionomidius Reitter, 1887:35. Type species: *Cryptophagus serricollis* Reitter, 1880, by monotypy.

Diagnosis.—Body form parallel-sided, moderately convex. Clypeus of male not notched. Antenna clubbed. Pronotum with anterior margin straight; lateral margin evenly serrate, not explanate or sinuate; angularity absent; prominent middle tooth absent; sublateral line absent; 10 lateral glandular ducts present. Hypomeron without field of pores. Prosternum without star-shaped glandular pores; prosternal process not vaulted. Ventrite 1 longer than remaining ventrites. Tarsal formula 554 in male.



Figs. 85-89. Metendosterna of Cryptophagidae. **85,** *Mnioticus gibbinsi.* **86,** *Anitamaria* sp. **87,** *Microphagus* sp. **88,** *Cryptafricus leleupi.* **89,** *Asternodea loebli.* (Scale bars = 0.1 mm).

Description.—Length 2.0-2.4 mm. Color of body light brown. Body form parallel-sided, moderately convex. Body setae short, suberect. Punctation of body and elytron confused. Glandular ducts of body not saccular. Head with line on vertex; frontoclypeal suture absent; subgenal spine well developed; gular sutures present; cephalic glandular ducts absent. Antenna clubbed; antennomeres slightly compact; last antennomere asymmetrical and subequal in length to that of penultimate. Mandible with 3 dorsal tubercles. Mentum with a transverse line or ridge. Eye reduced to a few facets; ocular setae absent. Pronotum parallel-sided with greatest width at middle; anterior margin of pronotum straight; sides not explanate; margin evenly serrate; pronotal angularity absent; prominent middle tooth absent; sublateral line absent; basal pits absent, not connected by a groove; median fold absent. Lateral margin of pronotum with 10 lateral glandular ducts. Hypomeron with notch near the procoxal cavity; field of pores absent. Prosternal process not vaulted, glandular duct absent. Anterior region of prosternum without glandular ducts. Mesepimeron with pit; ringlike cuticle absent. Mesosternum without parallel lines, width of mesosternal process equal to that of mesocoxa. Double knob articulation of meso- and metasternum present. Metasternum with median longitudinal line; pit below coxa absent; submesocoxal glandular duct present; discal glandular duct present. Metendosternite with anterior tendons approximate. Ventrite 1 longer than remaining ventrites; 2 discal glandular ducts present. Ventrites with 2 lateral glandular ducts on each side. Abdominal spiracles absent from segments 6 and 7. Prescutum with variolate microsculpture. Hind wing absent. Tibia with apical fringe of spines. Tarsomeres slightly lobed.

Male.— Clypeus not notched. Antennal segments not compact. Anterior portion of prosternum without star-like glandular ducts. Orientation of aedeagus vertical; tegmen with anterior arms separate or narrowly fused at distal ends. Ventrite 5 unmodified. Metatibia unmodified. Tarsal formula 554; tarsomeres 1-3 of pro- and mesotarsi dilated.

Diet.— Saprophagous (personal observation).

Distribution.— Caucasus Mountains, Europe.

Discussion.— The genus *Mnionomidius* is monotypic is a member of the *Henoticus* group and resembles members of *Henoticus*. It can be distinguished from other cryptophagines by the presence of 10 lateral pronotal glandular ducts and an eye reduced to a few facets.

Genus *Mnioticus* Coombs and Woodroffe
(Figs. 41, 85, 166, 185)

Mnioticus Coombs and Woodroffe, 1962:65. Type species: *Mnionomus hancocki* Scott, 1935, by original designation.

Diagnosis.—Body form parallel-sided, moderately convex. Clypeus of male not notched. Antenna clubbed. Pronotum with anterior margin straight; lateral margin unmodified; not explanate or sinuate; angularity absent; middle tooth absent; sublateral line absent; 1 lateral glandular duct present. Hypomeron with or without field of pores in males. Prosternum without star-shaped glandular pores; prosternal process not vaulted. Ventrite 1 equal to remaining ventrites. Tarsal formula 555 in male.

Description.—Length 2.5-4.0 mm. Color of body light, dark, or red brown, gray. Body parallel-sided, moderately convex. Body setae apressed, short. Punctation of body and elytron confused. Glandular ducts of body not saccular. Head with line with line on vertex; frontoclypeal suture absent; subgenal spine poorly developed; gular sutures present; cephalic glandular ducts present. Antenna clubbed; antennomeres slightly compact; last antennomere asymmetrical and subequal in length to that of penultimate. Mandible with 3 dorsal tubercles. Mentum with transverse line or ridge. Eye well developed, prominent; ocular setae present. Pronotum parallel-sided with greatest width at middle; anterior margin straight; sides not explanate; margin unmodified; angularity absent; prominent middle tooth absent; sublateral line absent; basal pronotal pits present, connected by a groove; medial fold present or absent. Lateral margin of pronotum with 1 lateral glandular duct. Hypomeron with notch near the procoxal cavity; field of pores present or absent. Prosternal process not vaulted, glandular duct absent. Anterior region of prosternum without glandular ducts. Mesepimeron with pit; ringlike cuticle absent. Mesosternum without parallel lines; width of mesosternal process 2/3 that of mesocoxa. Double knob articulation of meso- and metasternum present. Metasternum with median longitudinal line; pit below mesocoxa present or absent; submesocoxal glandular duct present or absent; discal glandular duct absent. Metendosternite with anterior tendons widely separate. Ventrite 1 equal in length to that of remaining ventrites; 1 discal glandular duct present. Ventrites with 2 lateral glandular ducts on each side. Abdominal spiracles absent from segments 6 and 7. Prescutum with variolate microsculpture. Hind wing absent. Tibia with apical fringe of spines. Tarsomeres slightly lobed.

Male.— Clypeus not notched. Antennal segments not compact. Anterior portion of prosternum without star-like glandular ducts. Orientation of aedeagus vertical; tegmen with anterior arms separate or narrowly fused at distal ends. Ventrite 5 unmodified. Metatibia unmodified. Tarsal formula 555; tarsomeres 1-3 of pro- and mesotarsi dilated.

Diet.— Fungal spores and hyphae (personal observation).

Habitat.— Leaf litter, rotting logs (Scott 1935; label data).

Distribution.— Montane east Africa.

Discussion.— The genus *Mnioticus* contains six species originally described as members of the genus *Mnionomus* (which is synonymous with *Cryptophagus*; see discussion under *Cryptophagus*) and were placed here by Coombs and Woodroffe (1962).

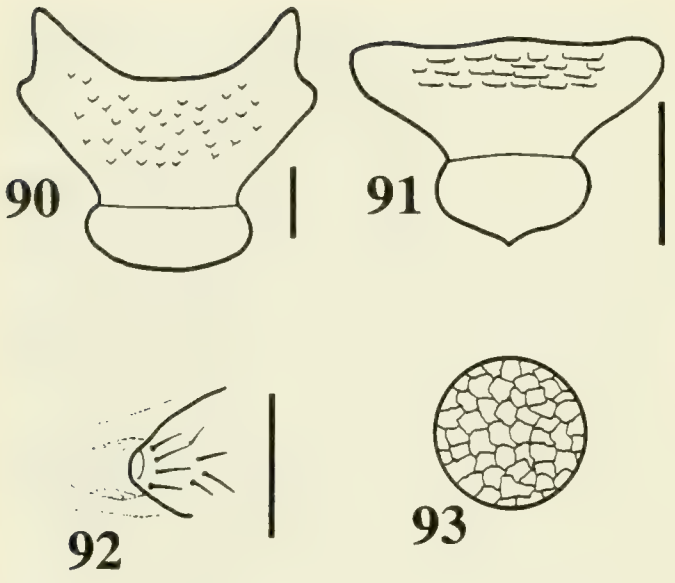
Members of *Mnioticus* are similar to some species of *Henoticus* in montane east Africa (see discussion under *Henoticus*). Members of *Mnioticus* appear to be monophyletic based on a combination of characters including the length of ventrite 1 equal to each of the remaining ventrites. *Mnioticus* is phylogenetically placed in the *Henoticus* group of genera and is sister taxon to *Telmatophilus*.

Genus *Myrmedophila* Bousquet
(Fig. 190)

Myrmedophila Bousquet, 1989:8. Type species: *Emphylus americana* LeConte, 1879, by original designation.

Diagnosis.—Body form parallel-sided, moderately convex. Clypeus of male not notched. Antenna clubbed. Pronotum with anterior margin straight; lateral margin evenly serrate, not explanate or sinuate; angularity present; prominent middle tooth present; sublateral line absent; 2 lateral glandular ducts present. Hypomeron without field of pores. Prosternum without star-shaped glandular pores; prosternal process not vaulted. Ventrite 1 longer than remaining ventrites. Tarsal formula 555 in male.

Description.—Length 1.9-2.6 mm. Color of body red brown. Body form parallel-sided, moderately convex. Body setae apressed, short. Punctation of body and elytron confused. Glandular ducts of body not saccular. Head with line on vertex; frontoclypeal suture absent; subgenal spine well developed; gular sutures present; cephalic glandular ducts absent. Antenna clubbed; antennomeres slightly compact; last antennomere asymmetrical and subequal in length to that of penultimate. Mandible with 3 dorsal tubercles. Mentum with transverse ridge. Eye well developed; ocular setae present. Pronotum parallel-sided with greatest width at middle; anterior margin straight; sides not explanate; margin unmodified; angularity present; prominent middle tooth present; sublateral line absent; basal pits present, not connected by a groove; median fold absent. Lateral margin of pronotum with 2 lateral glandular ducts. Hypomeron with a notch near the procoxal cavity; field of pores absent. Prosternal process not vaulted; glandular duct present. Anterior region of prosternum with glandular ducts. Mesepimeron with pit; ringlike cuticle absent. Mesoster-



Figs. 90-93. Morphological features of Cryptophagidae. **90,** *Micrambe* sp. (Africa), pteronotum (Scale bar = 0.1 mm). **91,** *Sternodea* sp. (Mexico), pteronotum (scale bar = 0.1 mm). **92,** *Seratomaria vulgaris*, metasternal pit (scale bar = 0.05 mm). **93,** *Amydropa clarki*, close-up of cuticle (diagrammatic).

num without parallel lines; width of mesosternal process 2/3 that of mesocoxa. Double knob articulation of meso- and metasternum present. Metasternum with median longitudinal line; pit below coxa present; submesocoxal glandular duct present; discal glandular duct present. Metendosternite with anterior tendons approximate. Ventrite 1 longer than remaining ventrites; 1 discal glandular duct present. Ventrites with 2 lateral glandular ducts on each side. Abdominal spiracles present on segments 1-7. Prescutum with variolate microsculpture. Hind wing present; cell absent; all veins present. Tibia with apical fringe of spines. Tarsomeres slightly lobed.

Male.— Clypeus not notched. Antennal segments not compact. Anterior portion of prosternum with star-like glandular ducts. Orientation of aedeagus vertical; tegmen with anterior arms separate or narrowly fused at distal ends. Ventrite 5 with small depressions. Metatibia unmodified. Tarsal formula 554; tarsomere 1 of all tarsi dilated.

Diet.— Saprophagous (personal observation).

Habitat.— *Formica* ant nests (Bousquet 1989).

Distribution.— Western North America.

Discussion.— The genus *Myrmedophila* is monotypic. Ljubarsky (1992d) discussed the generic status of this genus and suggested that it is a member of *Cryptophagus*. However, based on cladistic analysis, placing *Myrmedophila* in *Cryptophagus* may create a paraphyletic grouping (see discussion under *Cryptophagus*).

Neohenoticus Leschen, new genus
(Figs. 32, 54, 76, 114, 191)

Type species: *Neohenoticus palmerae* Leschen, new species

Diagnosis.—Body form parallel-sided, moderately convex. Antenna clubbed. Clypeus of male not notched. Pronotum with anterior margin straight; lateral margin irregularly serrate, not explanate or sinuate; angularity absent; prominent middle tooth absent; sublateral line absent; 4 lateral glandular ducts present. Hypomeron with field of pores. Prosternum without star-shaped glandular pores; prosternal process not vaulted. Ventrite 1 longer than remaining ventrites. Tarsal formula 554 in male.

Description.—Length 1.7-2.0 mm. Color of body light brown. Body parallel-sided, moderately convex. Body setae biseriate, erect, decumbent. Punctation of body and elytron confused. Glandular ducts of body not saccular. Head with line on vertex; frontoclypeal suture absent; subgenal spine well developed; gular sutures present; cephalic glandular ducts present. Antenna clubbed; antennomeres slightly compact; last antennomere asymmetrical and subequal in length to that of penultimate. Mandible with 2 dorsal tubercles. Mentum with a transverse line or ridge. Eye well developed, prominent; ocular setae present. Pronotum parallel-sided with greatest width at middle; anterior margin straight; side not explanate; margin irregularly serrate; angularity absent; prominent middle tooth absent; sublateral line absent; basal pits present, connected by a groove; median fold absent. Lateral margin of pronotum with 4 glandular ducts. Hypomeron with a notch near the procoxal cavity; field of pores present. Prosternal process not vaulted; glandular duct present. Anterior portion of prosternum with glandular ducts; star-like glandular pores absent. Mesepimeron with pit; ringlike cuticle absent. Mesosternum without parallel lines; width of mesosternal process equal to that of mesocoxa. Double knob articulation of meso- and metasternum absent. Metasternum with median longitudinal line; Metasternal pit below coxa present; submesocoxal glandular duct present; discal glandular duct present. Metendosternite with anterior tendons approximate. Ventrite 1 longer than remaining ventrites; 1 discal glandular duct present. Ventrites with 2 lateral glandular ducts on each side. Abdominal spiracles absent from segments 6 and 7. Prescutum with variolate microsculpture. Hind wing present; cell formed by a merging of CuA_2 and CuA_{3+4}+AA_{1+2} present; vein CuA_{3+4} absent. Tibia with apical fringe of spines. Tarsomeres slightly lobed below.

Male.— Clypeus not notched. Antennal segments not compact. Anterior portion of prosternum without star-like glandular ducts. Orientation of aedeagus vertical; tegmen with anterior arms separate or narrowly fused at distal ends. Ventrite 5 unmodified. Metatibia unmodified. Tarsal formula 554; tarsomeres 1-3 of pro- and mesotarsi dilated.

Habitat.— A single specimen was collected by beating rotten *Nothofagus* branches.

Distribution.— Chile.

Discussion.— The genus *Neohenoticus* is monotypic, is placed in the *Henoticus* group and is unique among members of Cryptophagini in having four lateral pronotal glandular ducts. It most closely resembles species of *Henoticus* which lack the lateral pronotal glandular ducts.

Etymology.— The generic name is derived from the root word *Henoticus*, a genus that the type species closely resembles, and the Greek word neos, meaning new.

Neohenoticus palmerae Leschen, new species
(Figs. 32, 54, 76, 114, 191)

Description.— Length 1.70- 2.00 mm (n = 13). Color of body light brown. Punctation dense, average width of puncture 0.002 mm. Body setae of long biseriate setae, decumbent and erect; average length 0.008 mm. Head densely punctate, punctures separated by about 1/2 diameter; interantennal distance = 0.018 mm. Eye prominent, coarsely faceted, preocular ridge present. Antenna elongate, extending beyond base of pronotum; antennomere relative lengths 8:9:6:6:5:5:5:5:7:7:10. Pronotum about 0.70 x as long as wide (PL/MPW = 0.64 - 0.75 , x = 0.70); depth = 0.31 - 0.38, x = 0.34 mm. Lateral margin of pronotum with 7-10 irregularly spaced teeth at side; punctures of disk separated by about 1/3-1/2 diameter. Prosternal process equal in length to anterior portion of prosternum; posterior margin rounded. Elytra about 1.51 x as long as wide (EL/MEW = 1.42 - 1.59, x = 1.22) and 2.81 x as long as pronotum (EL/PL = 2.60 - 3.08, x = 2.81); punctures separated by 1 diameter. Mesepimeron without a deep pit. Metasternal process evenly arcuate. Aedeagus as in Fig. 114.

Discussion.— As *Neohenoticus palmerae* is the only member of the

genus *Neohenoticus*, it can be distinguished from other members of Cryptophagini by the characters in the key to genera and diagnosis of the genus.

Etymology.— Named for Laura Palmer, who died an unnecessary and brutal death.

Type.— Holotype, with labels as follows: "Chile: Osorno; Puyehue Nat. Park, Antillanca Rd., 18-20.XII.84, S & J Peck. 500-1000m, carnetting, HOLOTYPE *Neohenoticus palmerae* R. Leschen 1994" (CNIS).

Paratypes.— 14. CHILE. 1, BW, FC Bowditch coll (MCZ). ARAUCO. 1, Rinconada, 25 m, 37°53'S, 73°18W, 8 Nov. 1994, R. Leschen, C. E. Carlton, #069, ex beating *Nothofagus* (SEMC). CAUTIN. 1, 15 km NE Villarica, Flor del Lago 14.XII.84 - 10.II.85. S & J Peck, 300m, FIT, *Nothofagus* forest. MALLECO. 2, Princesa 20 km W Curacautin, 12.XII.84 - 16.II.85. S & J Peck, FIT, 1000m, *Nothofagus* forest (CMN); 9 (1 on microslide), Puren Contulmo Natur. Mon., 11.XII.84 - 13.II.85, S & J Peck, FIT, 350 m, mixed evergr. forest (ANIC, CMN, RLC, SEMC, MANC).

Genus *Paramecosoma* Curtis
(Fig. 95)

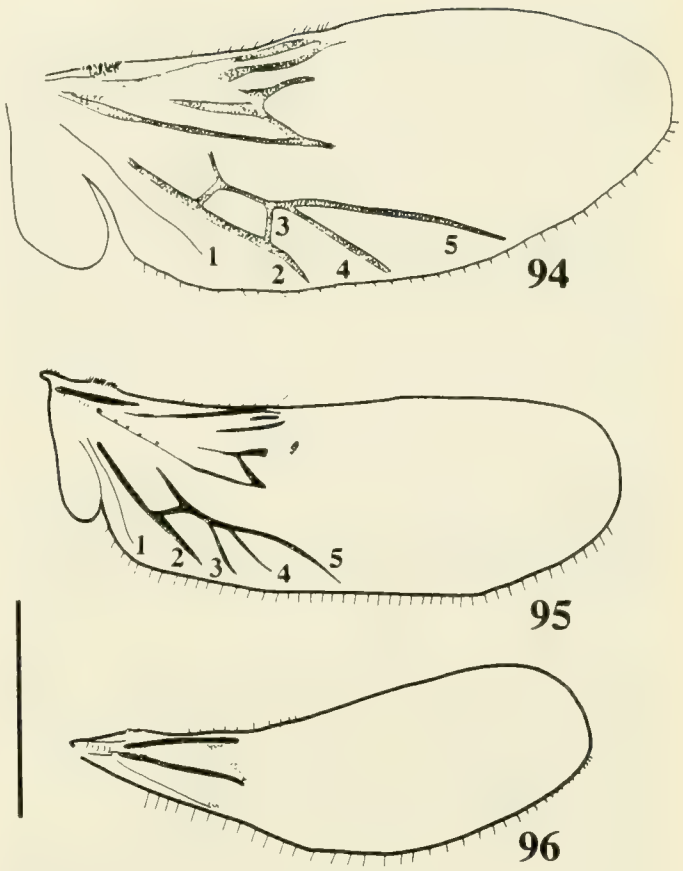
Paramecosoma Curtis, 1833:186. Type species: *Paramecosoma bicolor* Curtis, 1833, by monotypy.

Diagnosis.—Body form parallel-sided, moderately convex. Clypeus of male not notched. Antenna clubbed. Pronotum with anterior margin straight; lateral margin sinuate, not serrate or explanate; angularity present; prominent middle tooth absent; sublateral line absent; 3 lateral glandular ducts present. Hypomeron without field of pores. Prosternum with star-shaped glandular pores in male; prosternal process not vaulted. Ventrite 1 longer than remaining ventrites. Tarsal formula 554 in male.

Description.— Length 2.0-2.4 mm. Color of head, pronotum and venter dark brown; elytra red brown; mouthparts and antennae light brown. Body parallel-sided, moderately convex. Body setae short, decumbent. Punctation of body and elytron confused. Glandular ducts of body not saccular. Head with line on vertex; frontoclypeal suture absent; subgenal spine poorly developed; gular sutures present; cephalic glandular ducts absent. Antenna clubbed; antennomeres slightly compact; last antennomere asymmetrical and subequal in length to that of penultimate. Mandible with 3 dorsal tubercles. Mentum with a transverse line or ridge. Eye well developed, prominent; ocular setae present. Pronotum parallel-sided with greatest width at middle; anterior margin straight; sides not explanate; margin sinuate; angularity present; prominent middle tooth absent; sublateral line absent; basal pits absent; median fold present. Lateral margin of pronotum with 3 lateral glandular ducts. Hypomeron with notch near the procoxal cavity; field of pores absent. Prosternal process not vaulted; glandular duct present. Anterior region of prosternum with glandular ducts; star-like glandular pores present. Mesepimeron with pit; ringlike cuticle absent. Mesosternum without parallel lines; width of mesosternal process 2/3 that of mesocoxa. Double knob articulation of meso- and metasternum present. Metasternum with median longitudinal line; pit below coxa absent; submesocoxal glandular duct present; discal glandular duct absent. Metendosternite with anterior tendons approximate. Ventrite 1 longer than remaining ventrites; 1 discal glandular duct present. Ventrites with 2 lateral glandular ducts on each side. Abdominal spiracles present on segments 1-7. Prescutum with variolate microsculpture. Hind wing present; cell absent; all veins present. Tibia with apical fringe of spines. Tarsomeres slightly lobed below.

Male.— Clypeus not notched. Antennal segments not compact. Anterior portion of prosternum with star-like glandular ducts. Orientation of aedeagus vertical; tegmen with anterior arms separate or narrowly fused at distal ends. Ventrite 5 unmodified. Metatibia unmodified. Tarsal formula 554; tarsomeres 1-3 of pro- and mesotarsi dilated.

Diet.— Saprophagous (personal observation).



Figs. 94-96. Wings of Cryptophagidae. **94,** *Telmatophilus americanus.* **95,** *Paramecosoma melanocephalum.* **96,** *Cryptogasterus lawrencei.* (Scale bar = 1.0 mm, 1 = AA_{3+4}, 2 = CuA_{3+4}+AA_{1+2}, 3 = MP_4+CuA_1, 4 = CuA_{3+4}, 5 = MP_3).

Habitat.— Leaf litter at the edge of streams and rivers (Falcoz 1929).

Larval descriptions.— Larvae not described.

Distribution.— Eurasia.

Discussion.— The genus *Paramecosoma* is monotypic. *Paramecosoma* is sister taxon to members of *Salebius* and can easily be distinguished by the slightly undulate lateral margin of the pronotum. The undulations are not as well developed as they are in members of *Salebius.*

Genus *Pteryngium* Reitter
(Fig. 187)

Pteryngium Reitter, 1887:34. Type species: *Dermestes crenatus* Fabricius, 1798, by monotypy.

Diagnosis.—Body form parallel-sided, dorsoventrally flattened. Clypeus of male not notched. Antenna clubbed. Pronotum with anterior margin straight; lateral margin serrate, not sinuate or explanate; angularity absent; prominent middle tooth absent; sublateral line absent; lateral glandular ducts absent. Hypomeron with field of pores in males. Prosternum without star-shaped glandular pores; prosternal process not vaulted. Ventrite 1 longer than remaining ventrites. Tarsal formula 554 in male.

Description.—Length 1.7-2.1 mm. Color of body light brown. Body parallel-sided, dorsoventrally flattened. Body setae long, decumbent. Punctation of body and elytron confused. Glandular ducts

of body not saccular. Head with line on vertex; frontoclypeal suture absent; subgenal spine; gular sutures present; cephalic glandular ducts present. Antenna clubbed; antennomeres slightly compact; last antennomere asymmetrical and subequal in length to that of penultimate. Mandible with 2 dorsal tubercles. Mentum with a transverse line or ridge. Eye well developed, prominent; ocular setae present. Pronotum parallel-sided with greatest width at middle; anterior margin straight; sides not explanate; margin evenly serrate; angularity absent; prominent middle tooth absent; sublateral line absent; basal pits present, not connected by a groove; median fold absent. Lateral margin of pronotum without glandular ducts. Hypomeron with a notch near the procoxal cavity; field of pores present in male. Prosternal process not vaulted; glandular duct absent. Anterior region of prosternum without glandular ducts. Mesepimeron with pit; ringlike cuticle absent. Mesosternum without parallel lines; width of mesosternal process greater than that of mesocoxa. Double knob articulation of meso- and metasternum present. Metasternum with median longitudinal line; pit below coxa absent; submesocoxal glandular duct present; discal glandular duct present. Metendosternite with anterior tendons approximate. Ventrite 1 longer than remaining ventrites; discal glandular duct absent. Abdominal glandular ducts absent. Abdominal spiracles absent from segments 6 and 7. Prescutum with variolate microsculpture. Hind wing present; cell absent; vein CuA_{3+4} absent. Tibia with apical fringe of spines. Tarsomeres slightly lobed.

Male.— Clypeus not notched. Antennal segments not compact. Anterior portion of prosternum without star-like glandular ducts. Orientation of aedeagus vertical; tegmen with anterior arms separate or narrowly fused at distal ends. Ventrite 5 unmodified. Metatibia unmodified. Tarsal formula 554; tarsomeres 1-3 of pro- and mesotarsi dilated.

Diet.— Fungal spores and hyphae (personal observation).

Habitat.— Rotting logs, lignicolous fungi (Falcoz 1929, Scheerpeltz and Höfler 1948; Lawrence, unpublished data).

Distribution.— northern and montane Holarctic.

Discussion.— The genus *Pteryngium* is monotypic and is distinguished from other members of Cryptophagini by its flattened body form. *Pteryngium* is phylogenetically placed at the base of the Cryptophagini and is similar in form to members of *Henoticus*.

Examination of the holotype of *Pteryngium duclouxi* Grouvelle (1916) from China reveals that it is a member of *Micrambe* (see discussion under *Micrambe*).

Genus *Salebius* Casey
(Figs. 42, 188)

Salebius Casey, 1900:87. Type species: *Salebius sexdentatus* Casey, 1900, by subsequent designation (Bousquet 1989:6).

Diagnosis.—Body form parallel-sided, moderately convex. Clypeus of male not notched. Antenna clubbed. Pronotum with anterior margin straight; lateral margin sinuate, not serrate or explanate; angularity present; prominent middle tooth absent; sublateral line absent; 3 lateral glandular ducts present. Hypomeron without field of pores. Prosternum with star-shaped glandular pores; prosternal process not vaulted. Ventrite 1 longer than remaining ventrites. Tarsal formula 554 in male.

Description.— Length 2.4-3.1 mm. Color of body light or dark brown. Body parallel-sided, moderately convex. Body setae long, decumbent. Punctation of body and elytron confused. Glandular ducts of body not saccular. Head with line on vertex; frontoclypeal suture absent; subgenal spine well developed; gular sutures present; cephalic glandular ducts absent. Antenna clubbed; antennomeres slightly compact; last antennomere asymmetrical and subequal in length to that of penultimate. Mandible with 3 tubercles. Mentum with transverse ridge. Eye well developed, prominent; ocular setae present. Pronotum parallel-sided with greatest width at middle; anterior margin straight; sides not explanate; margin sinuate; angularity present; prominent middle tooth absent; sublateral line absent; basal pits present, not connected by a groove; median fold present. Lateral margin of pronotum with 3 glandular ducts; not saccular. Hypomeron with notch near the procoxal cavity; field of pores absent. Prosternal process not vaulted; glandular duct present. Anterior region of prosternum with glandular ducts. Mesepimeron with pit; ringlike cuticle absent. Mesosternum without parallel lines; width of mesosternal process equal to that of mesocoxa. Double knob articulation of meso- and metasternum present. Metasternum with median longitudinal line; pit below coxa present; submesocoxal glandular duct present; discal glandular duct absent. Metendosternite with anterior tendons approximate. Ventrite 1 longer than remaining ventrites; 1 discal glandular duct present. Ventrites with 2 lateral glandular ducts on each side. Abdominal spiracles on segments 1-7. Prescutum with variolate microsculpture. Hind wing present; cell absent; all veins present. Tibia with apical fringe of spines. Tarsomeres slightly lobed.

Male.— Clypeus not notched. Antennal segments not compact. Anterior portion of prosternum with star-like glandular ducts. Orientation of aedeagus vertical; tegmen with anterior arms separate or narrowly fused at distal ends. Ventrite 5 unmodified. Metatibia unmodified. Tarsal formula 554; tarsomeres 1-3 of pro- and mesotarsi dilated.

Diet.— Fungal spores and hyphae (personal observation).

Habitat.— Leaf litter, on fungi (unpublished data).

Distribution.— Western North America.

Discussion.— The genus *Salebius* is composed of five species including one species recently described by Dajoz (1988) from Arizona.

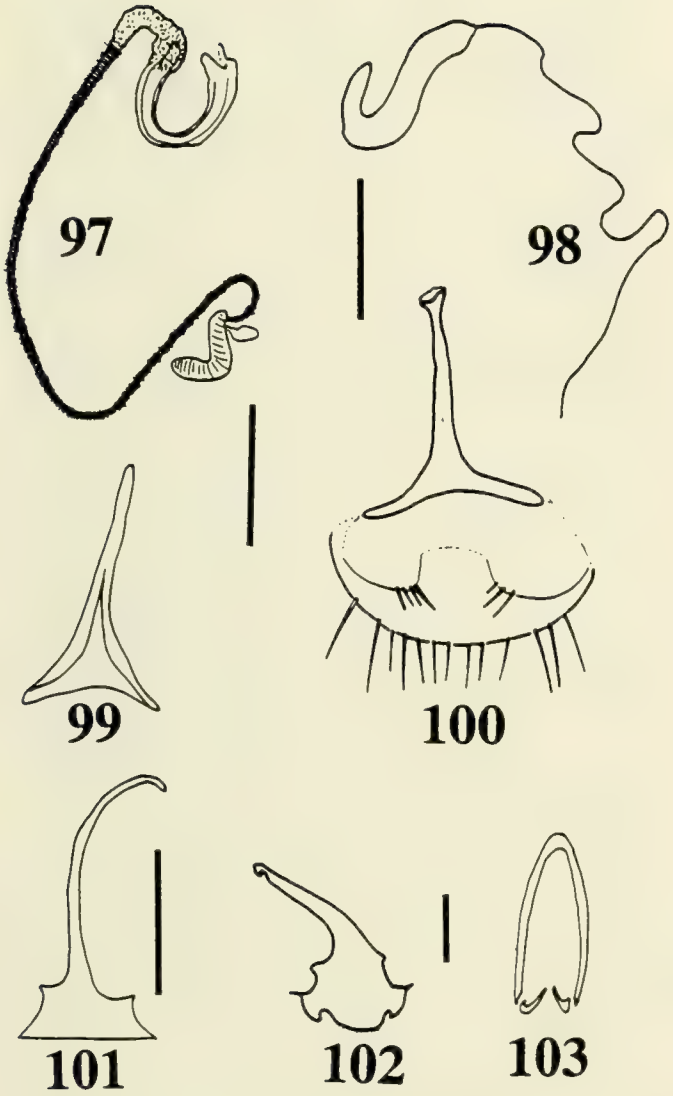
Because of the morphological similarities among members of *Salebius* and *Cryptophagus*, Bousquet (1989) suggested that *Salebius* may eventually be treated as a subgenus in *Cryptophagus*. Based on the cladistic analysis, however, placing *Salebius* in *Cryptophagus* would create a polyphyletic grouping (see discussion under *Cryptophagus*). *Salebius* is consistently placed as sister taxon to *Paramecosoma*, which have a sinuate lateral pronotal margin. The sinuate pronotal margin of members of *Salebius* is more developed than it is in members of *Paramecosoma*.

Genus *Serratomaria* Nakane and Hisamatsu
(Figs. 69, 92, 192)

Serratomaria Nakane and Hisamatsu, 1963:49. Type species: *Serratomaria tarsalis* Nakane and Hisamatsu, 1963, by original designation.

Diagnosis.—Body form parallel-sided, moderately convex. Clypeus of male not notched. Antenna clubbed. Pronotum with anterior margin straight; lateral margin irregularly serrate, not sinuate or explanate; angularity present; prominent middle tooth absent; sublateral line absent; 3 lateral glandular ducts present. Hypomeron without field of pores. Prosternum without star-shaped glandular pores; prosternal process not vaulted. Ventrite 1 equal in length to remaining ventrites. Tarsal formula 554 in male.

Description.—Length 1.7-2.0. Color of body variable, light or dark brown, bicolored. Body parallel-sided, moderately convex. Body setae decumbent, long or short, biseriate or uniseriate. Punctation of body and elytron confused. Glandular ducts of body saccular. Head with line on vertex; clypeal suture present or absent; subgenal spine poorly developed; gular sutures present; cephalic glandular ducts present. Antenna clubbed; antennomeres not compact; last antennomere asymmetrical and subequal in length to penultimate. Mandible with 2 dorsal tubercles. Mentum with a transverse line or ridge. Eye well developed, prominent; ocular setae present. Pronotum parallel-sided with greatest width at middle; anterior margin of pronotum straight; sides not explanate; margin irregularly serrate; angularity absent; prominent middle tooth absent; sublateral line absent; basal pronotal pits present, not connected by a groove; median fold absent. Lateral mar-



Figs. 97-103. Internal structures of Cryptophagidae. **97,** *Amydropa clarki*, spermatheca. **98,** *Microatomaria hintoni*, spermatheca. **99,** *Microphagus johnsoni*, spiculum gastrale of male. **100,** *Asternodea loebli*, spiculum gastrale and abdominal terga 8 and 9 of male. **101,** *Anitamaria thayerorum*, spiculum gastrale of male. **102,** *Cryptogasterus lawrencei*, spiculum gastrale of male. **103,** *Cryptafricus leleupi*, spiculum gastrale of male. (Scale bars = 0.1 mm).

gin of pronotum with 3 glandular ducts. Hypomeron with notch near the procoxal cavity; field of pores absent. Prosternal process not vaulted; glandular duct present. Anterior region of prosternum without glandular ducts. Mesepimeron with pit; ringlike cuticle present. Mesosternum without parallel lines; width of mesosternal process equal to that of mesocoxa. Double knob articulation of the meso- and metasternum absent. Metasternum with median longitudinal line; pit below coxa present; submesocoxal glandular duct present; discal glandular duct absent. Metendosternite with anterior tendons approximate. Ventrite 1 equal in length to remaining ventrites; 2 discal glandular ducts present. Ventrites with 1 lateral glandular duct on each side. Abdominal spiracles present on segments 1-7 or 1-6. Prescutum with variolate microsculpture. Hind wing present; cell formed by a merging of CuA_2 and CuA_{3+4}+AA_{1+2} present; vein MP_3 absent. Tibia with apical fringe of spines. Tarsomeres slightly lobed below.

Male.— Clypeus not notched. Antennal segments not compact. Anterior portion of prosternum without star-like glandular ducts. Aedeagus with anterior arms separate or narrowly fused at distal ends. Ventrite 5 unmodified. Metatibia unmodified. Tarsal formula 554; tarsomeres 1-3 of pro- and mesotarsi dilated.

Diet.—Fungal spores and hyphae (personal observation).

Habitat.— Bamboo leaves (Sasaji 1984).

Distribution.— Japan, southeast Asia.

Discussion.— The genus *Serratomaria* contains two described species; however, I have examined several undescribed species from southeast Asia and a revision of the genus would be useful. *Serratomaria* is monophyletic based on the presence of a unique combination of characters and is consistently placed in the cladograms as sister taxon to *Striatocryptus*.

Genus *Spaniophaenus* Reitter
(Fig. 182)

Spaniophaenus Reitter, 1875:4. Type species *Cryptophagus laticollis* Miller, 1858, by monotypy.

Catopochrotides Kieseritzky and Reichardt, 1936:693. Type species: *Catopochrotides termitophilus* Kieseritzky and Reichardt, 1936, by monotypy (first synonymized under the name *Spaniophaenus* by Ljubarsky 1992d:598).

Diagnosis.—Body form parallel-sided, moderately convex. Clypeus of male not notched. Antenna clubbed. Pronotum with anterior margin emarginate; lateral margin not modified not serrate, sinuate, or explanate; angularity present; prominent middle tooth absent; sublateral line absent; 1 lateral glandular ducts present. Hypomeron without field of pores. Prosternum with star-shaped glandular pores in male; prosternal process not vaulted. Ventrite 1 longer than remaining ventrites. Tarsal formula 554 in male.

Description.—Length 2.1-2.7 mm. Color of body dark brown. Body parallel-sided, moderately convex. Body setae long, suberect, apressed. Punctation of body and elytron confused. Glandular ducts of body not saccular. Head with line on vertex; frontoclypeal suture absent; subgenal spine well developed; gular sutures present; cephalic glandular ducts absent. Antenna clubbed; antennomeres not compact; last antennomere symmetrical and equal in length to penultimate. Mandible with 3 dorsal tubercles. Mentum with transverse ridge. Eye well developed, prominent; ocular setae present. Pronotum parallel-sided with greatest width at middle; anterior margin of pronotum emarginate; sides not explanate; margin unmodified; angularity present, poorly developed; prominent middle tooth absent; sublateral line absent; basal pits absent; median fold absent. Lateral margin of pronotum with 1 glandular duct. Hypomeron with notch near the procoxal cavity; field of pores absent. Prosternal process not vaulted; glandular duct present. Anterior region of prosternum with glandular ducts. Mesepimeron with pit; ringlike cuticle absent. Mesosternum without parallel lines; width of mesosternal process equal to or 2/3 that of mesocoxa. Double knob articulation of the meso- and metasternum present. Metasternum with median longitudinal line; pit below mesocoxae present or absent; submesocoxal glandular duct absent; discal glandular duct present. Metendosternite with anterior tendons approximate. Ventrite 1 longer than remaining ventrites; 1 discal glandular duct present. Ventrites with 2 lateral glandular ducts on each side. Abdominal spiracles present on segments 1-7. Prescutum with variolate microsculpture. Hind wing present or absent; cell absent; all veins present. Tibia with apical fringe of spines. Tarsi slightly lobed below.

Male.— Clypeus not notched. Antennal segments not compact. Anterior portion of prosternum with star-like glandular ducts. Orientation of aedeagus vertical; tegmen with anterior arms separate or narrowly fused at distal ends. Ventrite 5 unmodified. Metatibia unmodified. Tarsal formula 554; tarsomeres 1-3 of pro- and mesotarsi dilated.

Diet.— Saprophagous (personal observation).

Habitat.— Ant and termite nests (Falcoz 1929, Kistner 1982), under rocks, and bird nests (Ljubarsky 1992d).

Distribution.— Palaearctic.

Discussion.— The genus *Spaniophaenus* contains three species which were reviewed by Otero and Pazos (1995). Ljubarsky (1992d) recently synonymized the genus *Catopochrotides* with *Spaniophaenus*.

Spaniophaenus is a monophyletic taxon based on a unique combination of characters and is sister taxon to the species *Catopochrotus crematogastri*, also an inquiline in ant nests.

Genus *Spavius* Motschulsky
(Figs. 40, 186)

Spavius Motschulsky, 1844:51. Type species: *Cryptophagus glaber* Gyllenhal, 1808, by monotypy.

Emphylus Erichson, 1848:346. Type species: *Cryptophagus glaber* Gyllenhal, 1808, by monotypy (first synonymized under the name *Spavius* by Bousquet 1989:8).

Diagnosis.—Body form parallel-sided, moderately convex. Clypeus of male not notched. Antenna clubbed. Pronotum with anterior margin emarginate; lateral margin unmodified, not serrate, sinuate, or explanate; angularity present; prominent middle tooth absent; sublateral line absent; 1 lateral glandular duct present. Hypomeron without field of pores. Prosternum with star-shaped glandular pores in male; prosternal process not vaulted. Ventrite 1 longer than remaining ventrites. Tarsal formula 554 in male.

Description.—Length 2.0-2.7 mm. Color of body red brown. Body parallel-sided, moderately convex. Body setae sparse, short, apressed; longer setae present at tip of elytron and abdomen. Punctation of body and elytron confused, microsculpture strongly reticulate with very fine points. Glandular ducts of body not saccular. Head with line on vertex; frontoclypeal suture absent; subgenal spine well developed; gular sutures present; cephalic glandular ducts absent. Antenna clubbed; antennomeres compact; last antennomere asymmetrical and subequal in length to penultimate. Mandible with 3 dorsal tubercles. Mentum with a transverse line or ridge. Eye well developed, moderately prominent; ocular setae present. Pronotum parallel-sided with greatest width at middle; anterior margin emarginate; sides not explanate; margin unmodified; angularity present; prominent middle tooth absent; sublateral line absent; basal pits absent, not connected by a groove; median fold absent. Lateral margin of pronotum with 1 lateral glandular duct. Hypomeron with notch near the procoxal cavity; field of pores absent. Prosternal process not vaulted, glandular duct present. Anterior region of prosternum with glandular ducts. Mesepimeron with pit; ringlike cuticle absent. Mesosternum without parallel lines; width of mesosternal process 2/3 that of mesocoxa. Double knob articulation of meso- and metasternum present. Metasternum with median longitudinal line; pit below coxa absent; submesocoxal glandular duct present; discal glandular duct present. Metendosternite with anterior tendons approximate. Ventrite 1 longer than remaining ventrites; 1 discal glandular duct present. Ventrites with 2 lateral glandular ducts. Abdominal spiracles on segments 1-7. Prescutum with variolate microsculpture. Hind wing present; cell absent; all veins present. Tibia with apical fringe of spines. Tarsomeres slightly lobed below.

Male.— Clypeus not notched. Antennal segments not compact. Anterior portion of prosternum with star-like glandular ducts. Orientation of aedeagus vertical; tegmen with anterior arms separate or narrowly fused at distal ends. Ventrite 5 unmodified. Metatibia unmodified. Tarsal formula 554; tarsomeres 1-3 of protarsus and 1 of mesotarsus dilated.

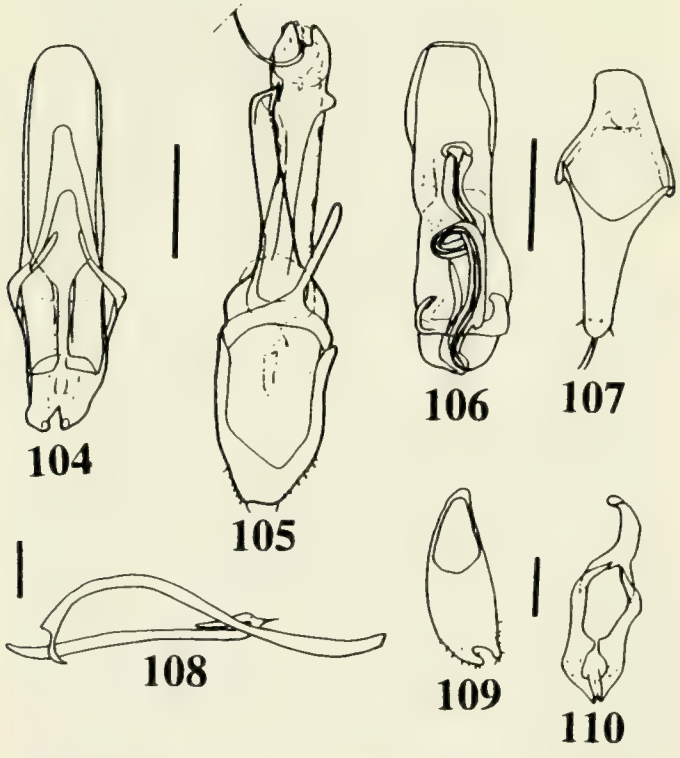
Diet.— Fungal spores and hyphae (personal observation).

Habitat.— Ant nests of the genus *Formica* (Eichelbaum 1907).

Larval descriptions.— *Spavius glaber* (Eichelbaum 1907).

Distribution.— Palaearctic.

Discussion.— The monotypic genus *Spavius* is a member of the *Cryptophagus* group and resembles species of *Cryptophagus* and *Myrmedophila*. *Spavius* can be distinguished from these genera by the emarginate anterior margin of the pronotum. Bousquet (1989) discussed the taxonomic status of the genus.



Figs. 104-110. Aedeagi of Cryptophagidae. **104,** *Anitamaria thayerorum*. **105,** *Microatomaria hintoni*. **106,** *Microphagus johnsoni*, basal piece. **107,** same, tegmen and endophallus. **108,** *Cryptafricus leleupi*. **109,** *Cryptogasterus lawrencei*, basal piece. **110,** same, tegmen and endophallus. (Scale bars = 0.1 mm).

Striatocryptus Leschen, new genus
(Figs. 26, 47, 48, 60, 70, 78, 117, 115, 120)

Type species: *Striatocryptus wilkinsoni* Leschen, new species

Diagnosis.—Body form parallel-sided, moderately convex. Clypeus of male not notched. Antenna clubbed. Pronotum with anterior margin straight; lateral margin explanate and evenly serrate (serrations poorly developed or absent in some species), not sinuate; angularity present or absent; prominent middle tooth absent; sublateral line absent; 1, 6, or 0 lateral glandular ducts present. Hypomeron with field of pores in male. Prosternum without star-shaped glandular pores; prosternal process not vaulted. Ventrite 1 equal to remaining ventrites. Tarsal formula 554 or 555 in male.

Description.—Length 1.5-1.7 mm. Color of body dark or chocolate brown; mouthparts, legs, and antenna yellow. Body form parallel-sided, moderately convex. Body setae erect, decumbent, biseriate. Punctation confused on body, seriate on elytra. Glandular ducts of body saccular or not. Head with line on vertex; frontoclypeal suture absent; subgenal spine poorly developed; gular sutures present; cephalic glands present. Antenna clubbed; antennomeres not compact; terminal antennomere asymmetrical and 2 times longer than that of the penultimate antennomere. Mandible

with 2 dorsal tubercles. Mentum with a transverse line. Eye well developed, prominent; ocular setae absent. Pronotum parallel-sided with greatest width at middle; anterior margin of pronotum straight; sides explanate; margin evenly serrate (serrations poorly developed or absent in some species); angularity present or absent; prominent middle tooth absent; sublateral line absent; basal pronotal pits present, not connected by a groove; median fold absent. Lateral margin of pronotum with 1, 6, or no glandular ducts. Hypomeron with a notch near the procoxal cavity; field of pores present. Prosternal process not vaulted; glandular duct present. Anterior region of prosternum without glandular ducts. Mesepimeron with pit; ringlike cuticle present. Mesosternum with or without parallel lines; width of mesosternal process 2/3 that of mesocoxa. Double knob articulation of meso- and metasternum absent. Metasternum with median longitudinal line; pit below coxa present; submesocoxal glandular duct present; discal glandular duct present or absent. Metendosternite with anterior tendons approximate. Ventrite 1 equal to remaining ventrites; 1 or 2 discal glandular ducts present. Ventrites with 1 lateral glandular duct. Abdominal spiracles absent from segments 6 and 7. Prescutum with variolate microsculpture. Hind wing present; cell formed by the merging of CuA_2 vein to the CuA_{3+4}+AA_{1+2} present or absent; veins MP_3 and CuA_{3+4} absent. Tibia without apical fringe of spines. Tarsomeres slightly lobed;

Male.— Clypeus not notched. Antennal segments not compact. Hypomeron with field of pores. Anterior portion of prosternum without star-like glandular ducts. Orientation of aedeagus vertical in body; tegmen with anterior arms fused and forming an elongate process. Ventrite 5 unmodified. Metatibia unmodified. Tarsal formula 554 or 555; tarsomeres 1-3 of all or pro- and mesotarsi dilated.

Diet.— Saprophagous (personal observation).

Habitat.— Leaf litter.

Distribution.— Asia, northern Africa.

Discussion.— The genus *Striatocryptus* is proposed for several undescribed species. Members of *Striatocryptus* are unique among Cryptophagidae because of the presence of uniseriate punctural striae on the elytron and an explanate pronotal margin. The explanate pronotal margin of genus 1 is not as flattened as it is in members of *Striatocryptus*. Based on cladistic information, *Striatocryptus* is sister taxon to *Serratomaria*.

Species can be distinguished from one another by the general shape of the pronotum, body coloration, punctation, tarsal formula of the male, and presence or absence of glandular ducts.

Etymology.— The generic name is a combination of the Latin word stria, that refers to the presence of punctate striae on the elytra, and the Greek word kryptos, referring to the family name Cryptophagidae.

Striatocryptus wilkinsoni Leschen, new species
(Figs. 26, 48, 60, 70, 78, 117, 120)

Description.— Length 1.88 mm. Punctation dense, average width of puncture 0.001 mm. Body setae of decumbent setae, not arising from slits; average length 0.009 mm. Glandular ducts not saccular. Head densely punctate, average width of puncture 0.002 mm, punctures separated by about 1 diameter; interantennal distance = 0.022 mm. Eye prominent, finely faceted. Antenna elongate, extending beyond base of pronotum; antennomere relative lengths 7:7:7:5:6:5:5:5:6:7:11. Pronotum about 0.78 x as long as wide (PL/MPW = 0.78). Pronotum without angularity; not strongly notched in basal portion; lateral margin of pronotum with 4 poorly defined evenly spaced teeth at side; punctures of disk separated by about 1 diameter, average width of puncture 0.001 mm, disk of basal portion without microsculpture. Prosternal process longer than anterior portion of prosternum; not subdepressed posteriorly behind procoxa. Elytra about 2.23 x as long as wide (EL/MEW = 2.23) and 2.31 x as long as pronotum (EL/PL = 2.31); punctures separated by 2 diameters. Mesepimeron with a deep pit containing several setae. Mesosternum with procoxal lines absent. Metasternum with subcoxal bead narrow, weakly impressed, joined at midline. Metasternal pit deep containing several setae. Metasternal process evenly arcuate. Disk of metasternum with 2 glandular ducts. Hind wing without wing cell. Tarsomeres 1-3 of all tarsi dilated. Aedeagus as in Fig. 117.

Discussion.— *Striatocryptus wilkinsoni* is distinguished from *S. polyglandis* by the absence of a pronotal angularity.

Etymology.— Named in honor of R. "Wilk" Wilkinson for inspiring me to pursue a career in biology and as a role model during my impressionable youth.

Type.— Holotype, male, with labels as follows: "Nepal: Lalitpur Distr. Phulcoki 2550 m 15.X.83, Smetana & Löbl, HOLOTYPE *Striatocryptus wilkinsoni* R. Leschen 1994"(MNHG, on microslide).

Striatocryptus polyglandis Leschen, new species
(Figs. 47, 115)

Description.— Length 1.87 mm. Punctation dense, average width of puncture 0.001 mm. Body setae of decumbent setae, arising from slits; average length 0.012 mm. Glandular ducts saccular. Head densely punctate, average width of puncture 0.002 mm, punctures separated by about 3/4 diameter; interantennal distance = 0.022 mm. Eye prominent, finely faceted. Antenna elongate, extending beyond base of pronotum; antennomere relative lengths 7:8:6:5:6:5:4:4:7:6:11. Pronotum about 0.66 x as long as wide (PL/MPW = 0.66). Pronotum with angularity; strongly notched in basal portion; lateral margin of pronotum with 5 evenly spaced teeth at side; punctures of disk separated by about 2/3 diameter, average width of puncture 0.002 mm, disk of basal portion without microsculpture. Prosternal process longer than anterior portion of prosternum; posterior portion slightly subdepressed behind procoxa. Elytra about 2.15 x as long as wide (EL/MEW = 2.15) and 2.53 x as long as pronotum (EL/PL = 2.53) longer than wide; punctures separated by 1.5 diameter. Mesepimeron with a deep pit containing several setae. Mesosternum with procoxal lines present. Metasternum with subcoxal bead narrow, deeply impressed, joined at midline. Metasternal pit deep containing several setae. Metasternal process evenly arcuate. Disk of metasternum with 1 glandular duct. Hind wing with cell. Tarsomeres 1-3 of pro- and mesotarsi dilated. Aedeagus as in Fig. 115.

Habitat.— Leaf litter.

Discussion.— *Striatocryptus polyglandis* can be distinguished from *S. wilkinsoni* by the shape of the pronotum and absence of an angularity.

Type.— Holotype, male, with labels as follows: "India: Kumaon (UP), Kathgodam Pres Haldemani, 600m, 6.X.79, HOLOTYPE *Striatocryptus polyglandis* R. Leschen 1994" (MNHG, on microslide).

Etymology.— The species name is a combination of the Greek word polys, meaning many, and the Latin word glandis, meaning gland, referring to the numerous glandular sacs in the body of this species.

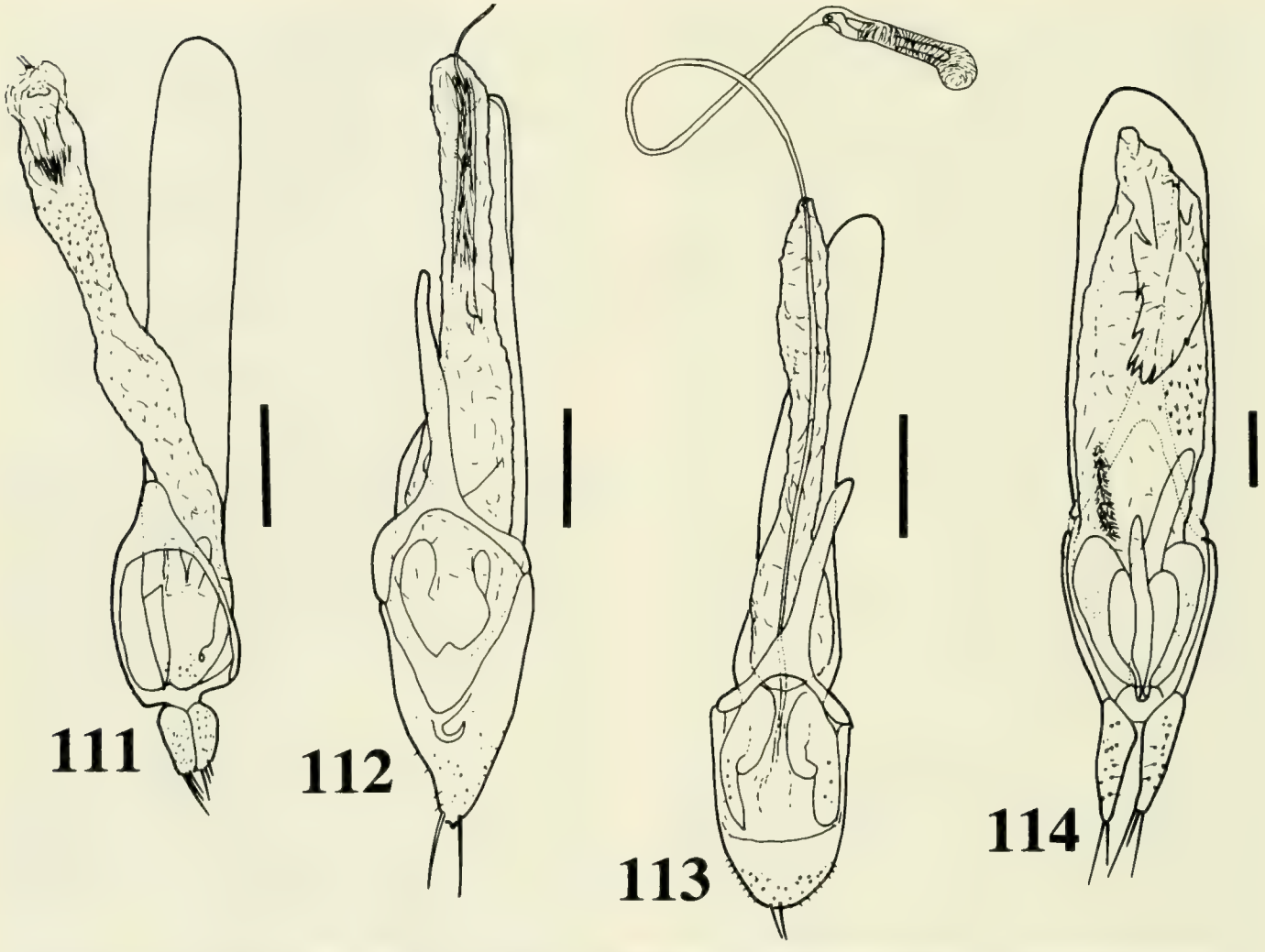
Genus *Telmatophilus* Heer
(Figs. 94, 124, 156)

Telmatophilus Heer, 1841:417. Type species: *Telmatophilus typhae* Fallén, 1802, here designated.

Hydrophytophagus Shuckard, 1839:173. Type species: *Telmatophilus typhae* Fallén, 1802, here designated.

Hydrophytophilus Erichson, 1846:82. (Unjustified emendation of *Hydrophytophagus* Shuckard).

Diagnosis.—Body form parallel-sided, moderately convex. Clypeus of male not notched. Antenna clubbed. Pronotum with anterior margin straight; lateral margin evenly serrate, not sinuate or sinuate; angularity absent; prominent middle tooth absent; sublateral line absent; lateral glandular ducts absent. Hypomeron without field of pores. Prosternum without star-shaped glandu-



Figs. 111-118. Aedeagi of Cryptophagidae. **111,** *Neopicrotus peckorum.* **112,** *Chilatomaria hillersae.* **113,** *Paratomaria crowsoni.* **114,** *Neohenoticus palmerae.* **115,** *Striatocryptus polyglandis.* **116,** *Amydropa clarki.* **117,** *Striatocryptus wilkinsoni.* **118,** *Asternodea loebli.* (Scale bars = 0.1 mm).

→

lar ducts; prosternal process not vaulted. Ventrite 1 longer than remaining ventrites. Tarsal formula 555 in male.

Description.—Length 2.1-2.8 mm. Color of body tan, dark or chocolate brown, dark or light brown, dark gray, elytron in one species infuscate. Body parallel-sided, moderately convex. Body setae short or long, apressed. Punctation of body and elytron confused. Glandular ducts of body not saccular. Head with line on vertex; frontoclypeal suture absent; subgenal spine poorly developed; gular sutures present, cephalic glandular ducts present. Antenna clubbed; antennomeres slightly compact; terminal antennomere asymmetrical and subequal to that of penultimate antennomere. Mandible with 2 dorsal tubercles. Mentum with transverse ridge. Eye well developed, prominent; ocular setae present. Pronotum parallel-sided with greatest width at middle; anterior margin of pronotum straight; sides not explanate; margin evenly serrate; angularity absent; prominent middle tooth absent; sublateral line absent; basal pits present, connected by a groove; median fold absent. Lateral margin of pronotum without glandular ducts. Hypomeron with a notch near the procoxal cavity; field of pores absent. Prosternal process not vaulted; glandular duct pres-ent. Anterior region of prosternum with glandular ducts. Mesepimeron with pit; ringlike cuticle absent. Mesosternum without parallel lines; width of mesosternal process 2/3 or equal to that of mesocoxa. Double knob articulation of meso- and metasternum present. Metasternum with median longitudinal line; pit below coxa present; submesocoxal glandular duct present; discal glandular duct absent. Metendosternite with anterior tendons approximate. Ventrite 1 longer than remaining ventrites; 1 discal glandular duct present. Ventrites with 2 lateral glandular ducts on each side. Abdominal spiracles absent from segments 6 and 7. Prescutum with variolate microsculpture. Hind wing present; cell formed by a merging of CuA_2 and CuA_{3+4}+AA_{1+2} present; vein MP_3 absent. Tibia with apical fringe of spines. Tarsomeres distinctly lobed.

Male.— Clypeus not notched. Antennal segments not compact. Anterior portion of prosternum without star-like glandular ducts. Orientation of aedeagus vertical; tegmen with anterior arms separate or narrowly fused at distal ends. Ventrite 5 modified. Metatibia modified. Tarsal formula 555.

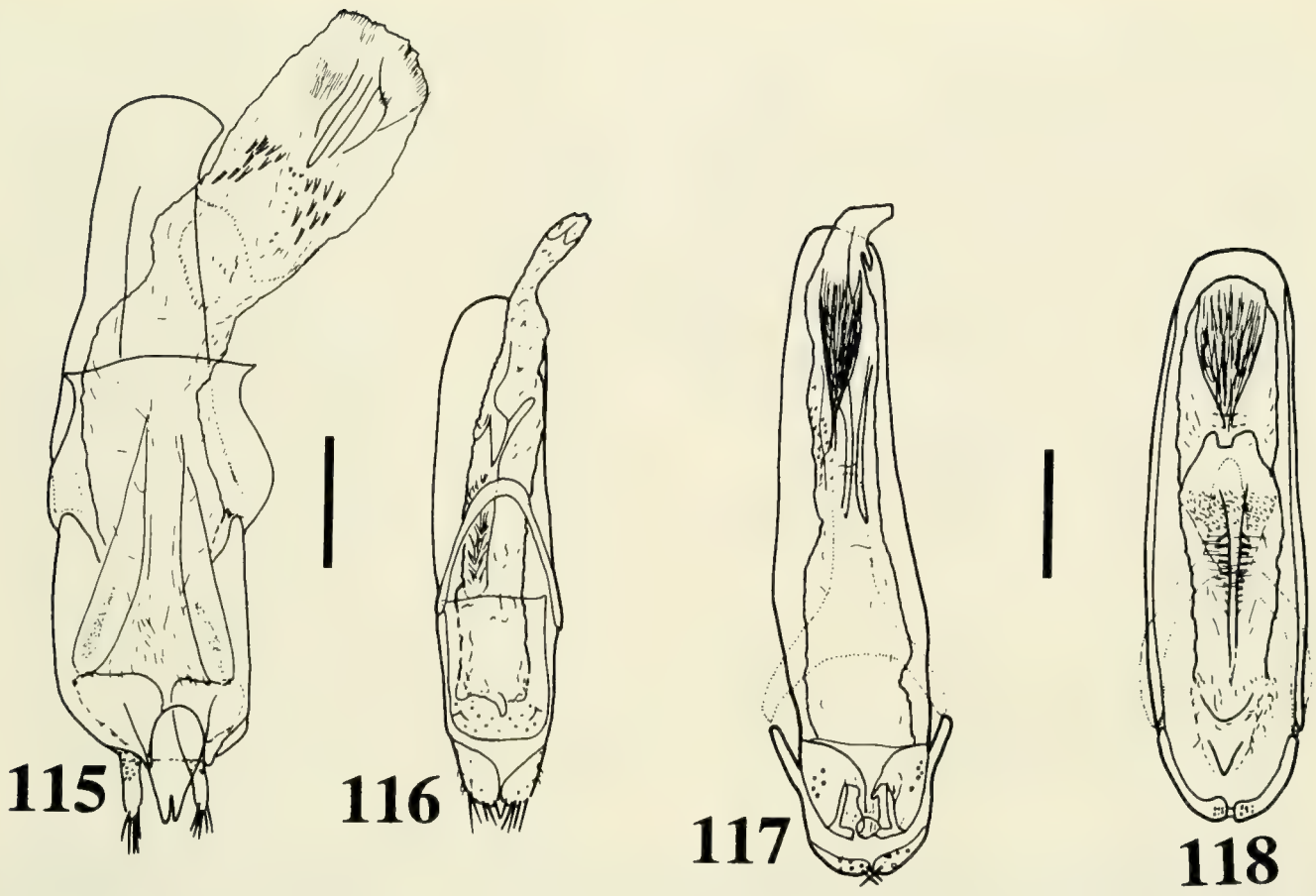
Diet.—Pollen of aquatic plants (personal observation).

Habitat.— Aquatic vegetation along ponds and lakes (Falcoz 1929).

Distribution.— Holarctic.

Larval descriptions.— *Telmatophilus brevicollis* Aubé (Perris 1877), *T. typhae* Fallén (Böving and Craighead 1931).

Discussion.— The genus *Telmatophilus* contains nine described



species and the only review available is for the European species (Karaman 1961). The genus is monophyletic based on a unique combination of characters including the presence of 555 tarsal formula in the male, diet of pollen, and presence of male secondary sexual characters. *Telmatophilus* is sister taxon to *Mnioticus*, and both are placed in the *Henoticus* group.

There is considerable variation of the male secondary sexual characteristics. The metatibia may have a well developed outer flange (*T. americanus* LeConte) or may be elbowed as it is in some species. In larger specimens of *T. caricis* (Olivier), the tibia may be more strongly elbowed than in smaller specimens. A deep triangular depression is present on the Ventrite 5 of males of *T. americanus*, while other species may have a shallow impression.

A phylogeny of the species would be useful for addressing questions about the evolution of host plant interactions and male secondary sexual characters.

TRIBE CRYPTOSOMATULINI

(Figs. 15, 16, 25, 39, 44, 66, 79, 84, 111, 121, 122, 132, 148, 157, 162, 170, 173, 194)

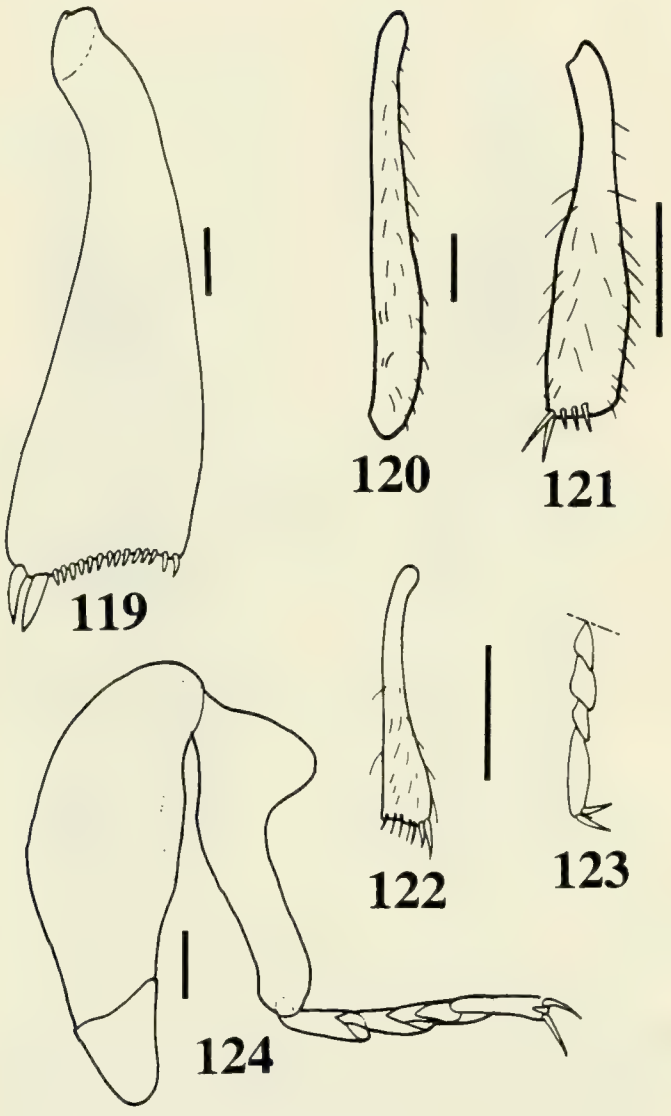
Cryptosomatulini Crowson, 1980:284. Type genus: *Cryptosomatula* Bruce, 1940.
Picrotini Crowson, 1980:282. Type genus: *Picrotus* Sharp, 1886.

Diagnosis— Conspicuous glandular ducts absent; microtubules present. Mandible without serrations on incisor lobe. Width of labial palpomere 1 equal to that of palpomere 2. Boss on front of head absent. Gular sutures present. Pronotum with lateral margin unmodified; basal pits of pronotum absent. Ventrite 5 without thickened setae or pegs. Orientation of aedeagus in body horizontal (vertical in some species). Tibia club-shaped (parallel-sided in some species).

Description.—Conspicuous glandular ducts absent, microglandular ducts present. Head without marginal ridge surrounding antennal concavity (present in *Thortus, Picrotus,* and *Neopicrotus*); boss on front of head absent (a carina is present in some *Thortus*); mandible without serrations on incisor lobe; width of labial palpomere 1 subequal to that of palpomere 2; gular sutures present. Pronotum with lateral margin unmodified (an angularity is present in *C. tasmanicus* and there is a "groove" present in many species); basal pits absent. Hypomeron with notch above procoxal cavity (absent in *C. tasmanicus, Cryptothelypterus, Chiliotis, Antarcticotectus,* and *Agnetaria*). Metasubcoxal line absent (present in *C. gibbipennis, Thortus,* and *Micrambina* from New Zealand). Ventrite 5 without thickened pegs or setae. Abdominal spiracles present on segments 1 - 5; spiracle on 7 modified (unmodified in *Thortus, Picrotus,* genus 2, and *Neopicrotus*). Microsculpture of prescutum variolate. Hind wing present (absent in *Cryptothelypterus, Neopicrotus, Thortus, Picrotus,* and Genus 2). Tibia club shaped (parallel-sided in *Chiliotis* and *Antarcticotectus*).

Male.— Aedeagal orientation in body vertical (variable in *Micrambina* from New Zealand). Tarsal formula 554.

Discussion.— Most species of this tribe are undescribed, and the tribe is not treated in detail here. A major study of the group must include a cladistic analysis to reconstruct relationships among the inclusive species and assign generic status to monophyletic groups of taxa. In the Appendix I have listed material examined and noted the generic placement of species. The tribe contains the follow-



Figs. 119-124. Legs of Cryptophagidae. **119,** *Antherophagus* sp., metatibia. **120,** *Striatocryptus wilkinsoni*, metatibia. **121,** *Thortus* sp., metatibia. **122,** *Neopicrotus peckorum*, metatibia. **123,** *Cryptafricus leleupi*, mesotarsus. **124,** *Telmatophilus americanus*, hind leg. (Scale bars = 0.1 mm).

ing genera: *Agnetaria, Antarcticotectus, Brounina, Chiliotis, Cryptosomatula, Cryptothelypterus, Micrambina, Neopicrotus* (described here), *Picrotus*, and *Thortus*.

Examination of the Broun collection deposited in the BMNH resulted in the **new synonymies** of *Picrotus pensus* Broun and *Picrotus sanguineus* Broun with *Picrotus thoracicus* Sharp. *Picrotus thoracicus* is unusual among Cryptosomatulini, and all of these specimens share in common a well developed marginal bead of the pronotum which is present only in *Atomaroides* and an undescribed species of *Picrotus* (which differs from *P. thoracicus* in several characters).

Below I describe a species belonging to a new genus which is strikingly different from other members of Cryptosomatulini I have examined.

Neopicrotus Leschen, new genus
(Figs. 15, 25, 39, 66, 79, 111, 122, 194)

Type species: *Neopicrotus peckorum* Leschen, new species

Diagnosis.— Body size small; form moderately convex; parallel-sided. Punctation absent in prosternal area. Antenna with 2 segmented club; inserted into a small concavity. Pronotum without angularity, setiferous tubercles, or serrations. Hind wing absent.

Description.— Length 1.0-1.3 mm. Color light brown. Body form moderately convex; parallel-sided. Body setae long, decumbent. Punctation in prosternal area absent. Microtubules present in body. Head constricted behind eye; with or without line on vertex; subgenal spine well developed; temporal ridge absent. Eye reduced to a few facets; preantennal ridge absent. Antenna with 2 segmented club; inserted into a small concavity; concavity with marginal ridge. Mandible with 2 dorsal tubercles. Mentum without a transverse line or ridge. Pronotum parallel-sided with greatest width at middle; margin unmodified; angularity absent. Hypomeron with notch near the procoxal cavity. Prosternum without star-like glandular ducts. Mesepimeron with pit. Mesosternum with parallel lines. Double knob articulation of meso- and metasternum present. Width of mesosternal process equal to that of mesocoxa. Metasternum without median longitudinal line. Metendosternite with anterior tendons widely separate. Ventrite 1 without metasubcoxal line; meta-intercoxal process about as long as wide. Posterior margin of Ventrite 5 without crenulations. Abdominal spiracles 1-7 present; 7 not modified. Orientation of aedeagus horizontal. Elytral impressions absent; subapical gape present. Hind wing reduced. Tibia club-shaped.

Male.— Aedeagal orientation in body horizontal. Tarsomeres 1-3 of pro- and mesotarsi dilated.

Habitat.— Leaf litter.

Distribution.— Chile.

Discussion.— The genus *Neopicrotus* is described for one species of an unusual Chilean cryptosomatuline with a 2-segmented antennal club. Other cryptosomatulines with a 2-segmented antennal club include *Agnetaria* (Tasmania) and *Picrotus* (New Zealand). *Neopicrotus* can be distinguished from *Agnetaria* by the lack of hind wing, antennal concavity with marginal ridge, body small and parallel-sided; and from *Picrotus* by the presence of a line on the vertex of the head, elongate body form, pronotum without a large marginal bead, and males without star-like glandular ducts on the proventer.

Etymology.— The generic name is derived from the root word *Picrotus*, a genus that the type species resembles, and the Greek word neos, meaning new.

Neopicrotus peckorum Leschen, new species
(Figs. 15, 25, 39, 66, 79, 111, 122, 194)

Description.— Length 1.00-1.29 mm (n = 2). Color of body light brown; mouthparts and antennal club light brown in some specimens. Punctation dense, average width of puncture 0.001 mm. Body setae long decumbent, some dorsal setae of base of head and elytra expanded at base of shafts; average length 0.004 mm. Head moderately densely punctate, punctures separated by about 1.5 diameters; dorsal base of head and venter areolate; interantennal distance = 0.014 mm. Eye not prominent, coarsely faceted, 10-12 facets at greatest length. Antenna elongate, extending slightly beyond base of pronotum; antennomere relative lengths 7:6:5:4:4:4:4:4:5:7:10. Pronotum very slightly wider anteriorly; about 0.84 x as long as wide (PL/MPW = 0.73 - 0.93 , x = 0.84); depth = 0.21 - 0.27, x = 0.24 mm; punctures of disk separated by about 1.5 diameters. Prosternal process equal in width to anterior portion of prosternum; sides parallel with posterolateral portion with small flanges; posterior margin slightly pointed. Elytra about 1.46 x as long as wide (EL/MEW = 1.32 - 1.51, x = 1.46) and 2.25 x as

long as pronotum (EL/PL = 1.90 - 2.54, x = 2.25); punctures separated by 1-5 diameters. Mesepimeron with a deep pit containing several setae; cuticle slightly ringed. Metasternal process evenly arcuate; sides relatively long.

Male.— Aedeagus as in Fig. 111.

Discussion.— *Neopicrotus peckorum* is the only flightless cryptosomatuline known from mainland Chilé. It can be distinguished from all other cryptosomatulines by the characters mentioned above.

Etymology.— Named in honor of S. Peck and J. Kukalova-Peck, persistent collectors of beetles.

Type.—Holotype, male, with labels as follows, "Chile: Valdivia Prov., 34 km NW La Union 700 m. 17.XII.1984. FMHD#85-921, litter mixed forest, S. & J. Peck, P#85-36, Berlese, HOLOTYPE *Neopicrotus peckorum* R. Leschen 1994" (FMNH).

Paratypes.— 9. CHILE: VALDIVIA. 4 (1 on microslide), same data as holotype (RALC, FMNH); 2, same data as holotype except, 7.11.1985, FMNH#85-997, mixed forest, P#85-114, (FMNH). CONCEPCION. 1, Estero Nonguén, Dic. 3, 1982, leg. T. Cekalovic (TC-115), collector C. van Nidek (ITZA); MALLECO. 2, Parque Nacional Nahuelbuta, 1450 m. Piedra del Aguila, 15.XII.1990, Agosti & Burckhardt #10a (MHNG).

TRIBE CAENOSCELINI

Caenoscelini Casey, 1900:103. Type genus: *Caenoscelis* Thomson, 1863.
Sternodeini Casey, 1900:103. Type genus: *Sternodea* Reitter, 1875.

Diagnosis— Conspicuous glandular ducts in body absent; microtubules absent. Mandible with serrations on incisor lobe. Width of labial palpomere 1 greater than that of palpomere 2. Boss on front of head present. Gular sutures absent. Pronotum with lateral margin unmodified; basal pits absent. Ventrite 5 with thickened setae or pegs. Orientation of aedeagus in body vertical. Tibia club-shaped.

Description.—Conspicuous glandular ducts in body absent; microtubules absent. Head with a marginal ridge surrounding antennal concavity; boss on front of head present; mandible with serrations on incisor lobe; width of labial palpomere 1 greater than that of palpomere 2; subgenal spine present; gular sutures absent. Pronotum with lateral margin unmodified. Hypomeron with notch absent above procoxal cavity. Metasubcoxal line present. Metasubcoxal line present (absent in *Dernostea*). Ventrite 5 with thickened pegs or setae. Abdominal spiracles present on segments 1-7; spiracle on 7 unmodified. Prescutal microsculpture elongate variolate. Hind wing absent (present in most species of *Caenoscelis*). Tibia club-shaped.

Male.— Orientation of aedeagus in body vertical. Tarsal formula 554 (555 in some Caenoscelis).

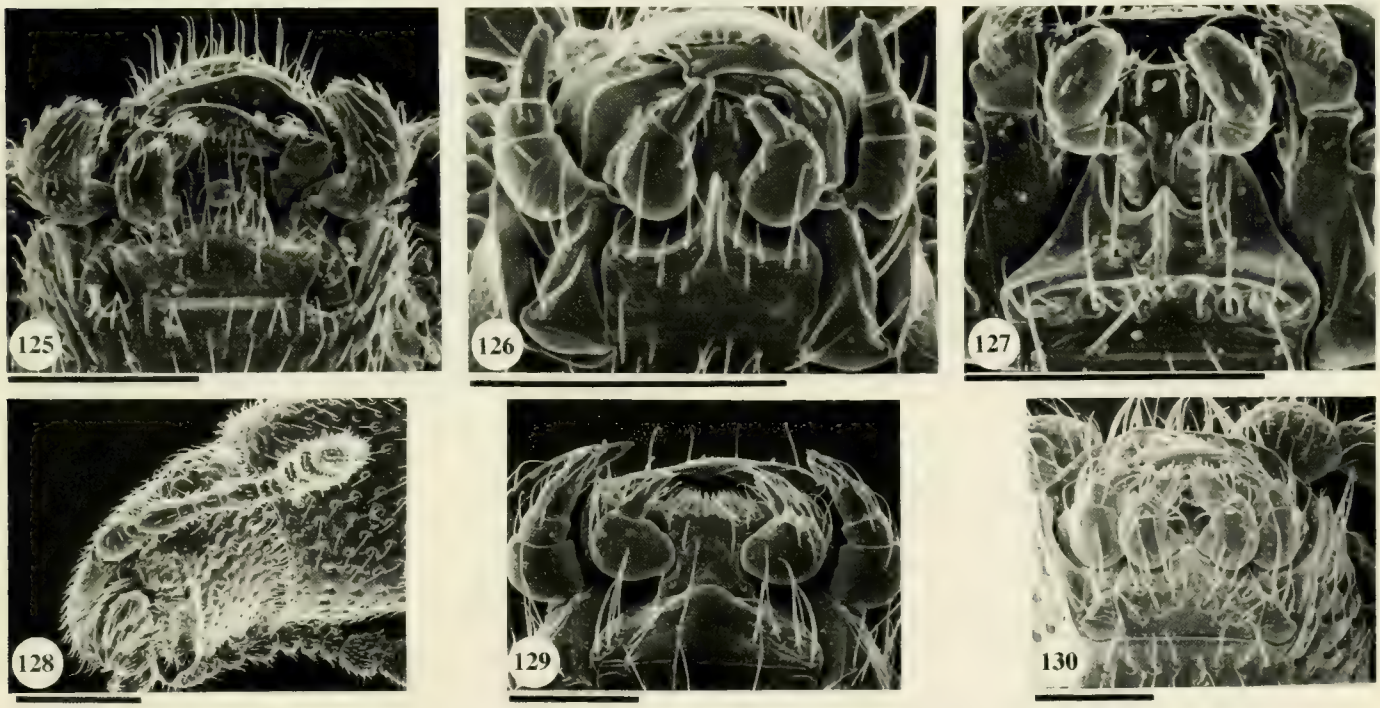
Discussion.— I recognize four genera in the tribe Caenoscelini.

Genus *Caenoscelis* Thomson
(Figs. 167, 189)

Caenoscelis Thomson, 1863:266. Type species: *Cryptophagus ferrugineus* C. R. Sahlberg, 1820, by monotypy.
Macrodea Casey, 1924:194. Type species: *Macrodea antennalis* Casey, 1924, by original designation (first synonymized by Bousquet 1989:13).

Diagnosis.—Body parallel-sided; pronotal sides parallel, greatest width at middle. Antennal club 3-segmented. Pronotum with sublateral lines (absent in one species from Asia). Prosternum without transverse pits. Hypomeron without antennal groove. Hind wing present (absent in some species).

Description.— Length 2.0-2.9 mm. Body form parallel-sided; moderately convex. Color light, dark, or red brown. Body setae variable, short, decumbent. Antenna with 3-segmented club.



Figs. 125-130. Ventral views of cryptophagid mouthparts. **125,** *Amydropa clarki*, mouthparts, ventral view (scale bar = 750 μm). **126,** *Ephistemus* sp. (Central America) (scale bar = 136 μm). **127,** *Henotiderus obesulum* (scale bar = 176 μm). **128,** *Amydropa clarki*, lateral view of head (scale bar = 100 μm). **129,** *Anitamaria* sp. (Australia) (scale bar = 60 μm). **130,** *Himascelis* sp. (Nepal) (scale bar = 75 μm).

Mandible with 2 dorsal tubercles, subapical serrations on both mandibles. Mentum with transverse line or ridge. Clypeus on same level as that of frons. Pronotum parallel-sided with greatest width at middle; sublateral line present (absent in one species); disk without transverse line. Hypomeron without antennal groove. Prosternum without deep transverse pits; prosternal process not vaulted. Mesepimeron with pits; ringlike cuticle absent. Mesosternum without parallel lines; width of mesosternal process 2/3 or equal to that of mesocoxa. Metendosternite with anterior tendons approximate. Ventrite 1 with metasubcoxal line present. Ventrite 5 with modified pegs or setae on its surface in both sexes. Hind wing present or absent; veins MP_3, MP_4+CuA_1, CuA_{3+4}, CuA_{3+4}+AA_{1+2} absent.

Male.— Antennomeres of flagellum enlarged in males of *C. antennalis*. Anterior portion of prosternum with star-like glandular ducts. Tarsal formula 555 or 554; tarsomeres 1-3 of pro- and mesotarsi dilated.

Diet.— Fungal spores and hyphae (personal observation).

Habitat.— Leaf litter, rotting wood (Johnson 1993).

Distribution.— Holarctic, east Africa (undescribed species).

Discussion.— The genus *Caenoscelis* contains 12 described species, and the North American fauna is presently being studied by C. Johnson.

Caenoscelis is monophyletic based on a unique combination of characters and is a basal member of Caenoscelini: Only a few species completely lack hind wings, unlike members of the remaining members of the tribe.

Genus *Dernostea* Sasaji
(Fig. 31)

Dernostea Sasaji, 1984:27. Type species: *Dernostea tanakai* Sasaji, 1984, by original designation.

Diagnosis.— Body form elongate oval; pronotal sides converging anteriorly, greatest width at base. Antennal club 1-segmented. Pronotum without sublateral lines. Prosternum with transverse pits. Hypomeron with antennal groove. Hind wing absent.

Description.— Length 1.2-1.4 mm. Body form elongate oval; moderately convex. Color light brown. Body setae short, decumbent. Antenna with 1-segmented club. Mandible without dorsal tubercles; subapical serrations on left mandible. Mentum without transverse line or ridge. Clypeus on same level as that of frons. Pronotum with sides converging anteriorly, greatest width at base; sublateral line absent; disk without transverse line. Hypomeron with antennal groove. Prosternum with deep transverse pits; prosternal process vaulted. Mesepimeron with pit; ringlike cuticle absent. Mesosternum with parallel lines; width of mesosternal process greater than that of mesocoxa. Metendosternite with anterior tendons widely separate. Metasubcoxal line absent. Hind wing reduced or absent.

Male.— Not studied.

Habitat.— Leaf litter (unpublished data).

Distribution.— Japan.

Discussion.— The genus *Dernostea* is monotypic; however, a similar species from southern California collected by K. Stephan is currently under study by C. Johnson and may be a member of this genus. *Dernostea* is sister taxon to *Himascelis*.

Genus *Himascelis* Sen Gupta
(Figs. 36, 130, 144)

Himascelis Sen Gupta, 1978:275. Type species: *Himascelis brunneus* Sen Gupta, 1978, by original designation.

Diagnosis.—Body form elongate oval; pronotal sides converging anteriorly, greatest width at base. Antennal club 2-segmented. Pronotum without sublateral lines. Prosternum with transverse pits. Hypomeron with antennal groove. Hind wing absent.

Description.— Length 1.3-1.5 mm. Body form elongate oval; not parallel-sided, greatest width at base. Color of body dark or light brown. Body setae short, decumbent. Antenna with 2-segmented club. Mandible without dorsal tubercles; subapical serrations on left mandible. Mentum with transverse line or ridge. Clypeus on lower plane than that of frons. Pronotum converging anteriorly, greatest width at base; sublateral line absent; disk without transverse line. Hypomeron with antennal groove. Prosternum with deep transverse pits; prosternal process vaulted; anterior portion without star-like glandular ducts. Mesepimeron with pit; ringlike cuticle present. Mesosternum with parallel lines; width of mesosternal process greater than that of mesocoxa. Metendosternite with anterior tendons widely separate. Ventrite 1 with metasubcoxal line. Hind wing absent.

Male.— Ventrite 5 with modified pegs. Tarsal formula 554; tarsomeres 1-3 of pro- and mesotarsi dilated.

Habitat.— Leaf litter (unpublished data).

Distribution.— Southeast Asia.

Discussion.— The genus *Himascelis* contains three described species from India; however, additional species have been collected in Nepal and Pakistan. *Himascelis* is sister taxon to *Dernostea*.

Genus *Sternodea* Reitter
(Figs. 18, 91, 193)

Sternodea Reitter, 1875:78. Type species: *Sternodea baudii* Reitter, 1875, by monotypy.

Diagnosis.—Body form elongate oval; pronotal sides converging anteriorly, greatest width at base. Antennal club 2-segmented. Pronotum without sublateral lines. Prosternum without transverse pits. Hypomeron without antennal groove. Hind wing absent.

Description.— Length 1.0-1.9 mm. Body form elongate oval; not parallel-sided. Color of body dark or light brown. Body setae long, decumbent, or erect, biseriate in some species. Antenna with 2-segmented club (1-segmented in a few species). Mandible without dorsal tubercles; subapical serrations on left mandible. Mentum with transverse line or ridge. Clypeus on same level as that of frons. Pronotum with sides converging anteriorly, greatest width at base; sublateral line absent; transverse line on disk present or absent. Hypomeron without antennal groove. Prosternum without deep transverse pits; prosternal process vaulted; anterior portion without star-like glandular ducts. Mesepimeron with pit; ringlike cuticle absent. Mesosternum without parallel lines; width of mesosternal process greater than that of mesocoxa. Metendosternite with anterior tendons widely separate. Ventrite 1 with metasubcoxal lines. Ventrite 5 with modified pegs or setae on surface of both sexes. Hind wing absent.

Male.— Tarsal formula 554 in male; tarsomeres 1-3 or 2 and 3 of protarsomere dilated.

Diet.— Fungal spores and hyphae (personal observation).

Habitat.— Leaf litter, rotting logs (unpublished data).

Distribution.— Palaearctic, Central America, Florida.

Discussion.— The genus *Sternodea* contains seven described species. Ljubarsky (1987a) reviewed the old world species and the new world species (with most species distributed in montane Central America) are currently being studied by C. Johnson. *Sternodea* is sister taxon to *Himascelis* + *Dernostea*.

SUBFAMILY ATOMARIINAE

Atomariinae LeConte, 1861:97. Type genus: *Atomaria* Stephens, 1829b.

Diagnosis.—Frontoclypeal suture present (absent in Hypocoprini). Transverse line on vertex of head absent (present in some Cryptafricini). Subgenal spine absent (present in *Alfieriella*) Mesometasternal articulation without double knob. Aedeagus with arms of tegmen broadly fused (fused apically or separate in *Alfieriella* and *Amydropa*); articulated parameres absent (present in *Amydropa* and *Alfieriella*). Tarsal formula of male 555 (444 in both sexes of some species).

Description.— Body form short or long, convex in most species.

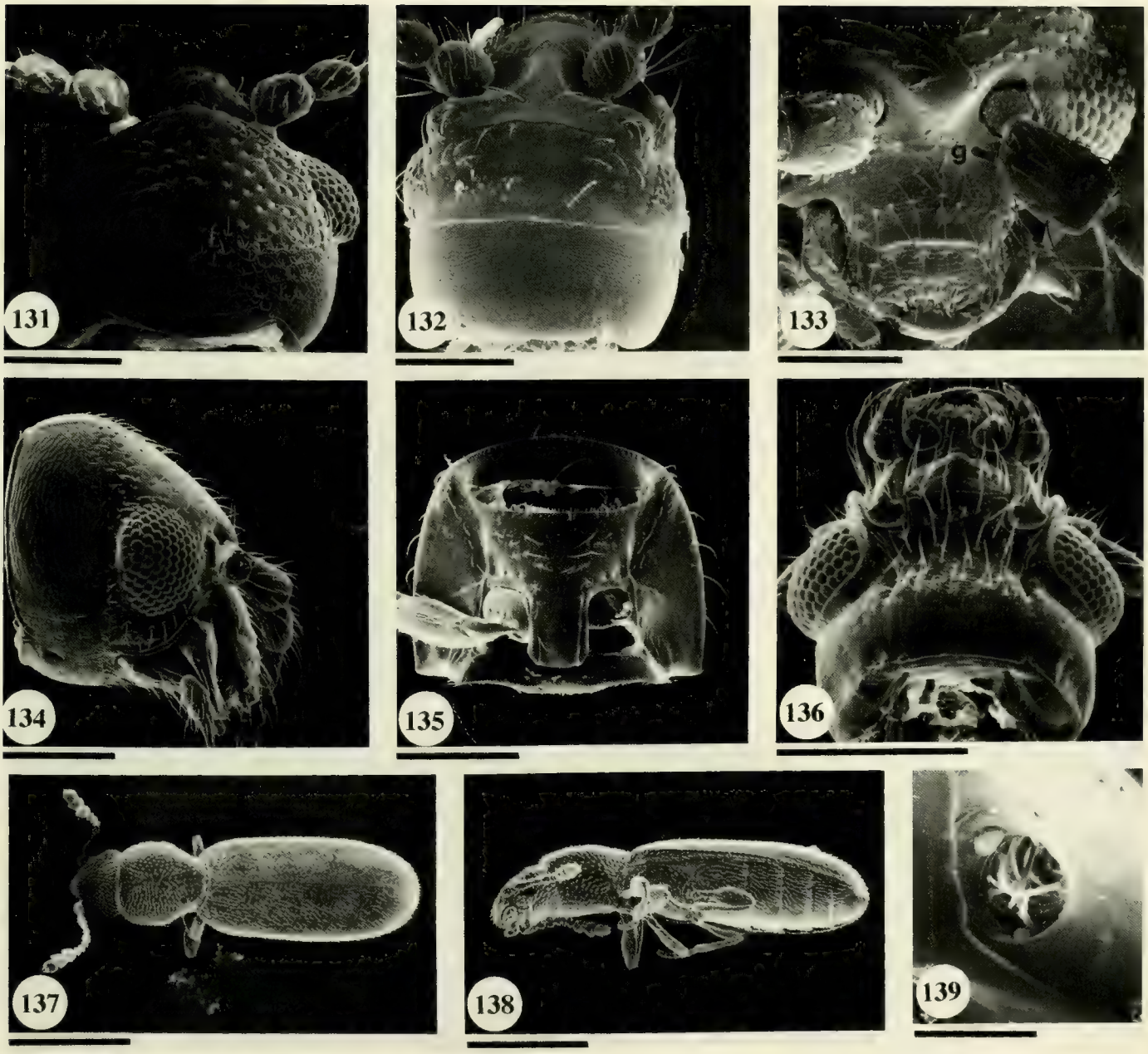


Fig. 131-139. Morphological features of Cryptophagidae. **131,** *Chilatomaria hillersae*, dorsal view of head (scale bar = 150 µm). **132,** *Thortus* sp., dorsal view of head (scale bar = 200 µm). **133,** *Atomaria* sp. (North America), anterior view of head (scale bar = 86 µm, g = glandular duct pore). **134,** Same, lateral view of head (scale bar = 176 µm). **135,** *Thortus* sp., proventer (scale bar = 0.33 mm). **136,** *Anitamaria* sp. (eastern Australia), ventral view of head (scale bar = 200 µm). **137,** *Amydropa clarki*, dorsal habitus (scale bar = 0.43 mm). **138,** Same, lateral habitus (scale bar = 0.38 mm). **139,** *Henotiderus obesulum*, mesepisternal pit (scale bar = 25 µm).

Conspicuous glandular ducts in body (absent in Hypocoprini and *Cryptafricus*); pores associated with setae in some Cryptafricini. Head with frontoclypeal suture (absent in Hypocoprini); width of palpomere 1 greater than (Atomariini and Cryptafricini) or subequal (*Alfieriella* and *Amydropa*) to palpomere 2; transverse ridge or line absent on mentum (present in *Chilatomaria*, some *Atomaria*, *Paratomaria*, and *Alfieriella*); subgenal spine absent (present in *Alfieriella*); gular sutures absent (present in some Cryptafricini and *Alfieriella*); transverse line on vertex of head absent (present in *Cryptogasterus* and *Anitamaria*); anterior arms of tentorium fused (separate in Hypocoprini); posterior portion of tentorium straight and broad (Atomariini) or narrow and straplike (Hypocoprini and Cryptafricini). Pronotum with lateral margin unmodified (angularity present in some Cryptafricini); basal pits absent. Hypomeron with notch above procoxal cavity absent (present in some members). Procoxal cavity internally open (closed in Cryptafricini); externally closed (open in *Hypocoprus* and some Atomariini). Prosternum without star-like glandular ducts. Mesepimeron without a distinct pit (present in some Atomariini). Meso-metasternal articulation without double knob. Metasternum

without longitudinal line (present in some Cryptafricini and Atomariini). Metasubcoxal lines absent (present in *Paratomaria, Microatomaria,* and some *Chilatomaria*). Wing with basal binding patch on wing poorly developed (well developed in some Atomariini). Tarsal formula 555 in both sexes (444 in *Cryptafricus* and *Atomaroides*). Tibia parallel-sided; apical spines present (absent in Hypocoprini and Cryptafricini).

Male.— Aedeagus without articulated parameres (present in some Hypocoprini); arms of tegmen broadly fused (narrowly fused or separate apically in *Alfieriella* and *Amydropa*).

Discussion.— In this revision I recognize 18 genera of Atomarinae placed among three tribes. The genus *Hypophagus* is treated as *incertae sedis* among Hypocoprini.

TRIBE HYPOCOPRINI

Hypocoprini Reitter, 1879:74. Type genus: *Hypocoprus* Motschulsky, 1839.

Diagnosis— Body form elongate. Conspicuous glandular ducts absent in body. Frons without tubercle. Posterior portion of tentorium narrow and straplike. Pronotal bead absent. Prosternum long in front of coxa. Tibia without apical spines.

Description.— Body form elongate. Conspicuous glandular ducts absent in body. Head with eye poorly developed; frons without tubercle; frontoclypeal suture absent; mandible without well developed sensory pores; width of labial palpomere subequal to or greater than (*Hypocoprus*) that of palpomere 2; anterior arms of tentorium separate; transverse ridge or line absent on mentum (present in *Alfieriella*); subgenal spine absent (present in *Alfieriella*); gular sutures absent (present in *Alfieriella*); line on vertex of head absent; posterior portion of tentorium narrow and straplike. Pronotum with lateral margin unmodified; marginal bead absent. Hypomeron without notch above procoxal cavity (present in *Hypocoprus*). Prosternum long in front of coxa; prosternal process short. Procoxal cavity internally open; externally closed (open in *Hypocoprus*). Metasternum without longitudinal line. Ventrite 5 evenly arcuate; asperities absent. Hind wing absent (present in *Hypocoprus*). Tarsal formula 555. Tibia without apical spines; 1 apical spur present (2 in *Amydropa*).

Male.—Arms of tegmen broadly fused (narrowly fused or separate at distal ends in *Alfieriella* and *Amydropa*). Endophallus rounded apically. Spiculum gastrale narrow.

Female.— Ovipositor well developed. Spiculum gastrale present. Spermathecal duct sclerotized (unsclerotized in *Alfieriella*).

Discussion.— In this revision I recognize four genera in the tribe Hypocoprini. Crowson (1980) discussed the genera *Alfieriella* and *Amydropa* and conditionally placed them in a subfamily Alfieriellinae without a description. Therefore, this name is *nomen nudum* (Pakaluk et al. 1995).

Genus *Alfieriella* Wittmer
(Figs. 14, 28, 196)

Alfieriella Wittmer, 1935:129. Type species: *Alfieriella rabinovitchi* Wittmer, 1935, by monotypy.

Cyprogenia Baudi, 1870:54, not Agassiz, 1852. Type species: *Cyprogenia denticulata* Baudi, by monotypy (first synonymized under the name *Alfieriella* by Ratti 1976:118).

Obenbergerodes Strand, 1936:168. Type species: *Cyprogenia denticulata* Baudi, 1870, by monotypy (first synonymized under the name *Cyprogenia* by Ratti 1976:118).

Diagnosis.— Microsculpture of body alveolate. Antennal club 1-segmented. Head with subgenal spines. Mesepimeron and mesosternum fused. Hind wing absent.

Description.— Length 1.3-2.2 mm. Body form elongate; more or less parallel-sided. Color light, dark, or red brown. Microsculpture alveolate. Body setae short or moderately elongate, decumbent. Head with subgenal spine well developed; gular sutures present. Antenna with 1-segmented club; terminal antennomere 2x the length of that of penultimate. Labium with width of palpomere 1 subequal to that of 2. Mentum with a transverse line or ridge. Procoxal cavity externally closed. Mesepimeron and mesosternum fused. Mesosternum without procoxal rests; width of mesosternal process 2/3 that of mesocoxa. Metendosternite with anterior tendons absent. Metepimeron widened posteriorly or parallel-sided. Ventrite 1 longer than remaining ventrites; meta-intercoxal process about as long as wide. Abdominal spiracle absent from segment 7. Prescutum with variolate microsculpture. Elytron with humeral tooth (present only in described species), subapical gape absent. Hind wing absent. Tibia with 1 apical spur.

Male.— Tegmen with anterior arms separate or narrowly fused at distal ends; parameres separate. Tarsomeres 1-3 of protarsus dilated.

Female.— Spermathecal duct unsclerotized.

Diet.— Saprophagous (personal observation).

Distribution.— Mediterranean, India.

Discussion.— Ratti (1976) reviewed the species of *Alfieriella* and discussed the taxonomic status of the genus. The genus listed as *Acryptus* in Sen Gupta and Crowson (1971) and the specimens labeled as "types" in the collection at BMNH are members of *Alfieriella. Alfieriella* and *Amydropa* are sister taxa.

Genus *Amydropa* Reitter
(Figs. 29, 46, 93, 97, 116, 125, 128, 137, 138, 147, 150)

Amydropa Reitter, 1877b:179. Type species: *Amydropa anophthalma* Reitter, 1877b, by monotypy.

Diagnosis.— Microsculpture of body alveolate. Antennal club 3-segmented. Head without subgenal spines. Mesepimeron and mesosternum fused. Hind wing absent.

Description.— Length 1.1-1.3 mm. Body form elongate; more or less parallel-sided; more or less convex. Color light brown. Microsculpture alveolate. Body setae short, sparse, apressed, or suberect. Head with subgenal spine poorly developed; gular sutures absent. Antenna with 3-segmented club; length of terminal antennomere 2x that of penultimate. Labium with width of palpomere 1 subequal to that of 2. Mentum without a transverse line or ridge. Procoxal cavity externally closed. Mesepimeron and mesosternum fused. Mesosternum without procoxal rests; width of mesosternal process less than 1/3 that of mesocoxa. Metendosternite with anterior tendons absent. Metepimeron parallel-sided or widened in apical half. Meta-intercoxal process about as long as wide. Ventrite 1 longer than remaining ventrites. Abdominal spiracles absent from segments 5 and 6. Prescutum without microsculpture. Elytron without humeral tooth, subapical gape absent. Hind wing absent. Tibia with 2 apical spurs.

Male.— Tegmen with anterior arms separate or narrowly fused at distal ends; parameres separate.

Female.— Spermathecal duct sclerotized, not convoluted.

Diet.— Saprophagous (personal observation).

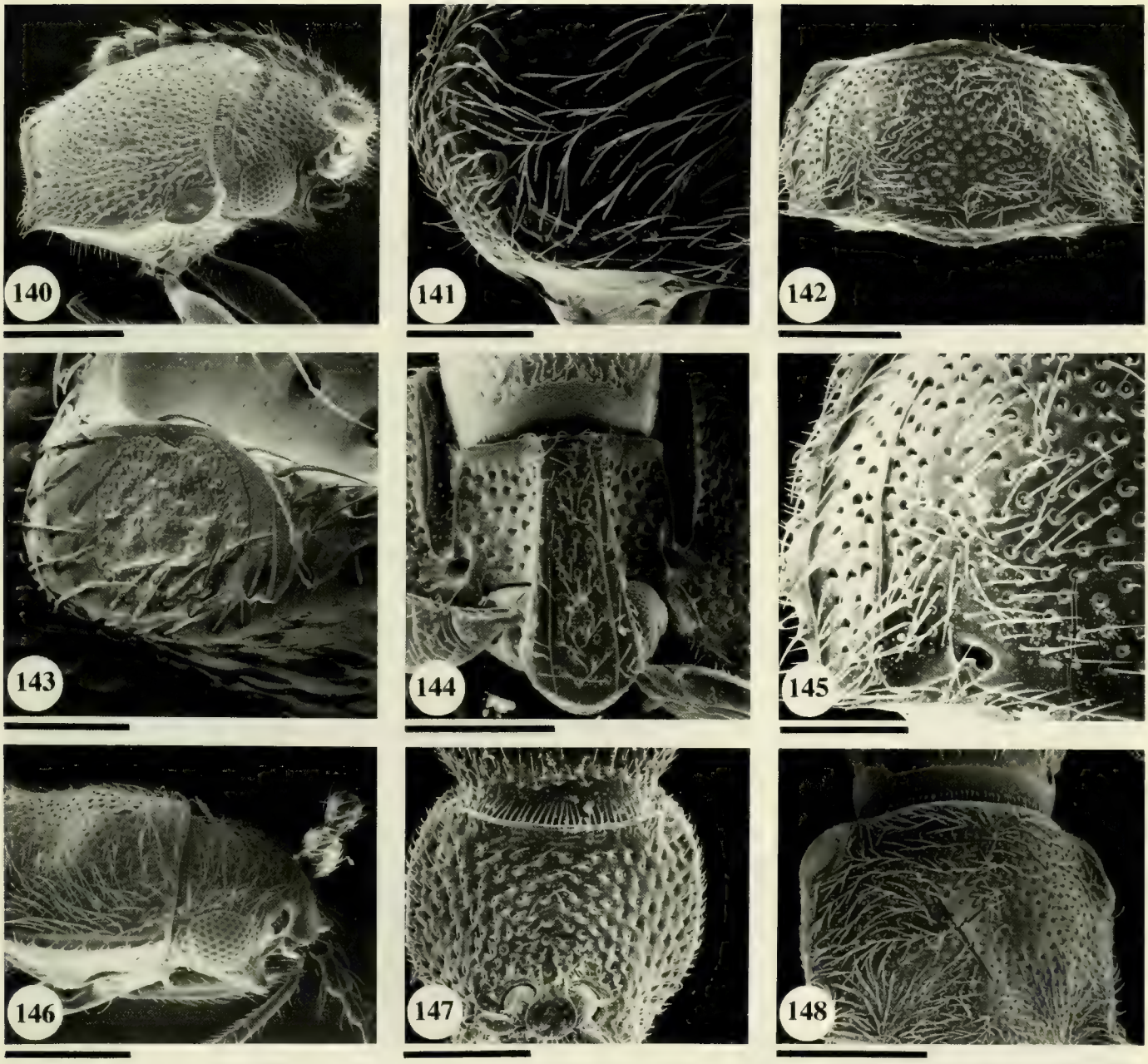
Habitat.— Leaf litter.

Distribution.— Baja California, Chile.

Discussion.— This genus was originally placed in the family Cucujidae (Reitter 1877b) and is listed in Hetschko (1930) in the subfamily Silvaninae. Two species are placed in *Amydropa*, one of which is described as new below. I have only encountered two specimens of *Amydropa* and these were labeled as *Amydropa integricollis* at BMNH and, therefore, I redescribe the species as below.

Amydropa is sister taxon to *Alfieriella* and differs from it by the presence of a 3-segmented antennal club. Although Reitter (1877b) characterized the genus as eyeless, tiny facets are visible with high magnification and in dissections.

The amphipolar distribution in the genus *Amydropa* is unusual because it involves only two species. Other cases of amphipolar distributions of cryptophagids (see Crowson 1980) usually involve sister taxa containing numerous species.



Figs. 140-148. Heads and pronota of Cryptophagidae. **140,** *Cryptophagus* sp., (North America), lateral view of head and pronotum (scale bar = 0.43 mm). **141,** *Anitamaria* sp. (Australia), pronotal angularity bearing a glandular duct pore (scale bar = 86 µm). **142,** *Henotiderus obesulum*, pronotum (scale bar = 0.27 mm). **143,** *Cryptophagus* sp. (North America), pronotal angularity with glandular secretion (scale bar = 43 µm). **144,** *Himascelis* sp. (Nepal), prosternum (scale bar = 176 µm). **145,** *Henotiderus obesulum*, pronotum (scale bar = 120 µm). **146,** *Chiliotis* sp. (Chile), lateral view of head and pronotum (scale bar = 0.33 mm). **147,** *Amydropa clarki*, proventer (scale bar = 120 µm). **148,** *Cryptophagus* nr. *tasmanicus*, pronotum (scale bar = 0.33 mm).

***Amydropa clarki* Leschen, new species**
(Figs. 93, 97, 116, 125, 128, 137, 138, 147, 150)

Description.— Length 0.87-1.07 mm (n = 10). Color of body light brown. Punctation moderately dense; average width of puncture 0.001 mm. Body setae of short decumbent setae; average length 0.002 mm. Head with punctures separated by about 1 diameter; interantennal distance = 0.011 mm. Eye not prominent, coarsely faceted, composed of 10 facets. Antenna moderately elongate, extending to basal 1/3 of pronotum; 11-segmented, antennomere relative lengths 4:3:1:1:2:1:2:2:2:3:4. Pronotum with greatest width in anterior half; about 1.02 x as long as wide (PL/MPW = 0.92 - 1.17, x = 1.02); depth = 0.12 - 0.17, x = 0.15 mm; punctures of disk separated by about 1 diameter. Prosternal process with posterior margin evenly arcuate. Metepisternum widened in posterior half. Elytra about 1.98 x as long as wide (EL/MEW = 1.79 -

2.09, x = 1.98) and 2.53 x as long as pronotum (EL/PL = 2.27 - 2.81, x = 2.53); punctures absent. Metasternal process evenly arcuate. Aedeagus as in Fig. 116.

Diet.— Saprophagous (personal observation).

Habitat.— Leaf litter.

Discussion.— This species is distributed in the desert of Baja California and can be distinguished from *A. anophthalmus* by the shape of the pronotum which is widened anteriorly and presence of an 11-segmented antenna. Hundreds of specimens have been collected in pitfall traps.

Etymology.— Named in honor of W. H. Clark, one of the collectors of these beetles.

Type.—Holotype, with labels as follows, "Mexico, Baja California Norte, 9km NW Rancho Santa Ines, Lat. 29 deg. 46 min N, Long 114 deg 46 min W, El: 550 m, Ethylene Glycol Pitfall Trap #7, 17 July 1991 to 26 May 1992, Coll. W. H. Clark, E. M. Clark, P. E. Blom & D. M. Ward, HOLOTYPE *Amydropa clarki* R. Leschen 1994"(ORMA).

Paratypes.— 171. BAJA CALIFORNIA: 47, same as Holotype except collected on May 26, 1992 and no trap # designated (SEMC, FMNH, ANIC, MANC, USNM, BMNH, ORMA); 84, same as Holotype except some in trap #3, #13, and #17; 10, 11.7 km East El Rosario, Lat 30 deg 4 min 30 Sec N, Long 115 deg 37 min 55 sec W, 180 m, Ethylene Glycol Pitfall Trap #2 and 4, 17 July 1991 to 26 May 1992, Coll W. H. Clark, E. M. Clark, P. E. Blom and D. M. Ward (ORMA); 3, SE base of Mesa El Tecolote, Lat 26 deg 59 min N Long 113 deg 26 min W, El 120 m, Ethylene Glycol Pitfall trap, 8 July 1991 to 28 May 1992, Coll. W. H. Clark, E. M. Clark, P. E. Blom and D. M. Ward; 4, Norte, Valle Montevideo La Laguna wash, Lat. 28 deg 55 min N Long 113 deg 44 min W, 380 m , 18 km W Bahia Los Angeles, Ethylene Glycol Pitfall trap #2, 14 July 1991 to 13 May 1992, Coll. W. H. Clark, E. M. Clark, P. E. Blom and D. M. Ward (ORMA); 1 Norte, 4.3 km NE Pozo Aleman, Lat 28 deg 14 min N Long 113 deg 21 min W, El 300 m, Ethylene Glycol Pitfall Trap #1, 15 June 1990 to 19 May 1992, Coll W. H. Clark, E. M. Clark, E. Blom and D. M. Ward (ORMA); 1, Norte, El Crucero, Lat 29 deg 16 min N, Long 114 deg 09 min W, Elevation 610 m, Ethylene Glycol Pitfall Trap #10, 17 July 1991 to 26 May 1992, Coll. W. H. Clark, E. M. Clark, P. E. Blom and D. M. Ward (ORMA); 1, Norte, KM 108,14 km NW Sta. Cecilia, Lat 30 deg 03 min N, Long 115 deg 16 min W, El. 600 m, Ethylene Glycol Pitfall Trap, 18 July 1991 to 28 May 1992, Coll. W. H. Clark, E. M. Clark, P. E. Blom and D. M. Ward (ORMA); 1, Norte, La Ramona, Lat 29 deg 48 min N, Long 115 deg 05 min W, Elevation 440 m, Ethylene Glycol Pitfall Trap #1, 3 July 1991 to 27 May 1992, Coll W. H. Clark, E. M. Clark, P. E. Blom and D. M. Ward (ORMA); 1 Norte, San Agustin, Lat 29 deg 56 min N, Long 114 deg 58 min W, Elevation 580 m, Ethylene Glycol Pitfall Trap #1, 16 July 1991 to 26 May 1992, Coll. W. H. Clark, E. M. Clark, P. E. Blom and D. M. Ward (ORMA); 18, Santa Catarina, 1 January 1989, W. Clark (RALC, MNHG, PARI).

Amydropa anophthalma Reitter
(Figs. 29, 46)

Description.— Length 0.92 - 1.04 mm (n = 2). Color of body yellow brown. Punctation dense on pronotum; average width of puncture 0.001 mm. Body setae of long decumbent setae; average length 0.003 mm. Head without punctures; interantennal distance = 0.012 mm. Eye not prominent, coarsely faceted, composed of 3 facets. Antenna moderately elongate, extending to basal 1/3 of pronotum; antenna 10-segmented, antennomere relative lengths 4:5:2:3:3:2:2:2:3:3:6. Pronotum with greatest width at middle; about 0.90 x as long as wide (PL/MPW = 0.86 - 0.94, x = 0.90); depth = 0.17 mm; punctures of disk separated by about less than 1 diameter. Prosternal process with posterior margin notched. Metepisternum parallel-sided. Elytra about 1.94 x as long as wide (EL/MEW = 1.82 - 2.06, x = 1.94) and 2.39 x as long as pronotum (EL/PL = 2.31 - 2.47, x = 2.39); punctures absent. Metasternal process evenly arcuate. Aedeagus not examined.

Discussion.— No specimens of this species were found in Reitter's collections at HUNG or NMNH which contain many type specimens of Cryptophagidae described by Reitter. In addition, requests for *Amydropa* material made to various European collections did not yield specimens. However, among cucujid material in the BMNH there were two specimens labeled as *Amydropa integricollis.* I was unable to locate this name in the literature except where it is mentioned as *A. integricolle* (Germain) after the description of *A. anophthalma* as a species "communicated" to Reitter (1877b). These specimens match Reitter's (1877b) original description and, therefore, I selected one of these as a neotype of *A. anophthalma* and the name *A. integricolle* is a *nomen nudum.* The species was originally described based on specimens collected in Chile, but the exact location is unknown.

Amydropa anophthalma can be distinguished from *A. clarki* by the shape of the pronotum and presence of a 10-segmented antenna.

Material examined.— Neotype, with labels as follows: CHILE (round, light blue), HW. 399 *Amydropa integricollis* (illegible), NEOTYPE *Amydropa anophthalma* Reitter R. Leschen 1994" (BMNH); 1, same data as neotype (on a microslide) (BMNH).

Genus *Hypocoprus* Motschulsky
(Fig. 195)

Hypocoprus Motschulsky, 1839:72. Type species: *Hypocoprus lathridioides* Motschulsky, 1839, here designated.

Myrmecinomus Chaudior, 1845:206. Type species: *Myrmecinomus hochhuthi* Chaudoir, 1845, by monotypy (first synonymized under the name *Hypocoprus* by Wollaston 1864:141).

Diagnosis.— Microsculpture of body areolate (body) and punctate (elytra). Antennal club 3-segmented. Head without subgenal spines. Mesepimeron and mesosternum separate. Hind wing present.

Description.— Length 1.0-1.3 mm. Body form elongate; more or less parallel-sided. Color light, dark, or red brown, black; elytron bicolored in some specimens. Microsculpture of body areolate (body) and punctate (elytra). Body setae moderately long, apressed, decumbent. Head with subgenal spine absent; gular sutures absent. Antenna with 3-segmented club; terminal antennomere subequal in length of that of penultimate. Labium with width of palpomere 1 greater than that of 2. Mentum without transverse line or ridge. Procoxal cavity externally open. Mesepimeron and mesosternum not fused. Mesosternum with procoxal rests; width of mesosternal process equal to that of mesocoxa. Metendosternite with anterior tendons approximate. Metepimeron parallel-sided. Ventrite 1 length equal to remaining ventrites; meta-intercoxal process wider than long. Abdominal spiracle absent from segment 7. Prescutum with variolate microsculpture. Elytron without humeral tooth, subapical gape present. Hind wing present; marginal setae present to level of RA+ScP vein; basal binding patch poorly developed or absent; veins MP_3, MP_4+CuA_1, CuA_{3+4}, CuA_{3+4}+AA_{1+2} absent. Tibia without apical fringe of spines; 1 apical spur present.

Male.— Tegmen with anterior arms broadly fused at distal ends; parameres absent. Tarsomeres 1-3 of protarsus dilated.

Female.— Spermathecal duct sclerotized.

Diet.— Fungal spores and hyphae (personal observation).

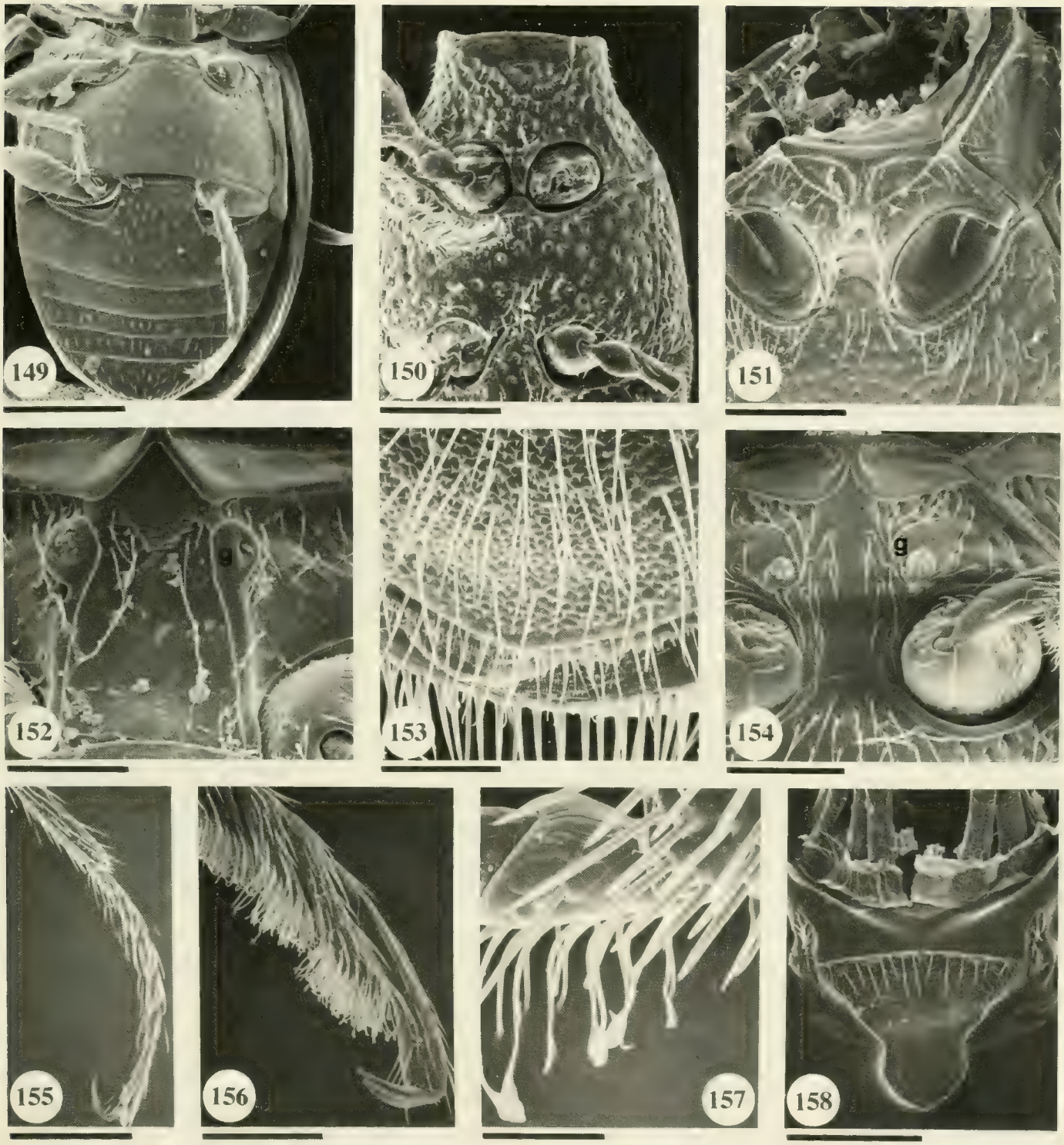
Habitat.—*Formica* ant nests, leaf litter, large mammal dung (Crowson 1955; J. L. Carr, personal communication; C. Johnson, personal communication).

Distribution.— Holarctic.

Discussion.— There are three species contained in the genus *Hypocoprus.* Based on a few dissections, there are no obvious characters separating *H. lathridioides* and *H. tenuis* Casey. *Hypocoprus* is sister taxon to *Alfieriella* and *Amydropa.*

Genus *Hypophagus* Ljubarsky

Hypophagus Ljubarsky, 1989:49. Type species: *Hypophagus epipedus* Ljubarsky, 1989, original designation.



Figs. 149-158. Morphological features of Cryptophagidae. **149,** *Ephistemus* sp. (Central America), ventral view of body (scale bar = 0.27 mm). **150,** *Amydropa clarki,* meso- and metasternum (scale bar = 86 μm). **151,** *Anitamaria* sp. (Australia), meso- and metasternum (scale bar = 136 μm). **152,** *Chilatomaria hillersae,* mesosternum (scale bar = 120 μm, g = glandular duct pore). **153,** *Anitamaria* sp. (Australia), abdominal sternite 5 (scale bar = 38 μm). **154,** *Paratomaria crowsoni,* mesosternum (scale bar = 120 μm, g = glandular duct pore with secretion). **155,** *Anitamaria* sp. (eastern Australia), metatarsus (scale bar = 136 μm). **156,** *Telmatophilus americanus,* mesotarsus (scale bar = 100 μm). **157,** *Chiliotis* sp. (Chile), male protarsus (scale bar = 30 μm). **158,** *Anitamaria* sp. (Australia), pteronotum (scale bar = 0.1 mm).

Discussion.— Although specimens of this genus were unavailable for study, examination of published illustrations suggests that it may be a member of Hypocoprini based on the following characters: body form elongate and parallel-sided, antennal insertions widely separate, prosternum long in front of procoxae, parameres articulate. *Hypophagus epipedus* looks superficially like a large species of *Hypocoprus* except that ventrite 1 is longer than remaining ventrites and the procoxal cavities are round and not slightly transverse.

TRIBE ATOMARIINI

Atomariini LeConte, 1861:97. Type genus: *Atomaria* Stephens, 1829b.
Ephistemini Casey, 1900:104. Type genus: *Ephistemus* Stephens, 1829a.
Salltiini Crowson, 1980:284. Type genus: *Salltius* Broun, 1893.

Diagnosis— Body form short or long, round in most species. Conspicuous glandular ducts present in body. Frons without tubercle. Posterior portion of tentorium straight and broad. Pronotal bead present. Prosternum short in front of coxa. Tibia with apical spines.

Description.— Body form short, oval in most species. Conspicuous glandular ducts present in body; pores not associated with setae. Head with eyes well developed; frontoclypeal suture present; frons without tubercle; mandible with well developed sensory pores (absent in *Atomaroides*); width of palpomere 1 greater than that of palpomere 2; gular sutures absent; anterior arms of tentorium fused; posterior portion of tentorium straight and broad. Pronotum with lateral margin unmodified; lateral bead present. Hypomeron with notch present above procoxal cavity (absent in most members of south temperate genera). Prosternum short in front of coxa; anterior glandular ducts present (absent in south temperate genera). Procoxal cavity internally open, externally closed (open in *Tisactia, Curelius, Ephistemus,* and *Ootypus*). Mesosternal glandular ducts present (absent in some species of *Chilatomaria*). Metasternum without longitudinal line (present in *Atomaroides, Paratomaria,* some specimens of *Salltius, Chilatomaria,* and *Atomaria*). Ventrite 5 evenly arcuate; asperities absent. Hind wing present or absent. Tibia with apical spines; 2 apical spurs present.

Male.— Aedeagus with arms of tegmen broadly fused; endophallus rounded apically. Spiculum gastrale broad.

Female.— Ovipositor well developed. Spiculum gastrale present. Spermatheca c-shaped (not c-shaped in *Salltius*); spermathecal duct unsclerotized (sclerotized in *Salltius, Microatomaria,* some *Atomaria,* and some *Chilatomaria*), coiled or not.

Discussion.— In this revision I recognize 10 genera in the tribe Atomariini.

Genus *Atomaria* Stephens
(Figs. 133, 164, 202)

Atomaria Stephens, 1829b:83. Type species: *Dermestes nigripennis* Paykull, 1798, by subsequent designation (Westwood 1840:14).
Anchicera Thomson, 1863:274. Type species: *Atomaria munda* Erichson, 1846, here designated.
Agathengis Gozis, 1886:10. Type species: *Atomaria fimetarii* Herbst, 1793 by original designation (first synonymized under the name *Atomaria* by Reitter 1887:36).
Grobbenia Holdhaus, 1903:354. Type species: *Atomaria fimetarii* Herbst, 1793, by monotypy (first synonymized under the name *Atomaria* by Johnson 1992:120).
Microum Wollaston, 1854:177. Type species: *Ephistemus alternans* Wollaston, 1854, by monotypy (first synonymized under the name *Atomaria* by Wollaston 1857:62).

Diagnosis.— Body form elongate or oval; pronotum more or less parallel-sided, greatest width at middle. Antennal club 3-segmented. Cephalic glandular ducts not fused in middle. Antennal grooves on head and prosternum absent. Pronotum with lateral marginal bead narrow. Prosternum without parallel lines; anterior glands present. Mesosternal glands not opening onto a callus. Metasubcoxal lines absent. Tarsal formula 555; tarsomeres not strongly lobed.

Description.— Length 1.0-2.2 mm. Color of body variable, unicolorous, bicolored in some species. Body form parallel-sided, elongate or oval. Body setae variable, sparse, dense, short, long, decumbent, apressed. Prosternal area with punctation. Head not constricted behind eye; boss on front of head present; clypeus on lower plane than that of frons; antennal grooves absent; cephalic glandular ducts present, not fused at middle. Antenna with 3-segmented club; antennomere 11 subequal to that of 10; antennomere 3 up to 2x the length of 4; shape of funicle conical and curved or cylindrical. Mandible with 2 dorsal tubercles; basal sensory pores present. Mentum with median process; transverse line or ridge present or absent. Eye prominent; ocular setae present. Pronotum parallel-sided, greatest width at middle; marginal bead narrow. Hypomeron with notch near procoxal cavity. Prosternal process without parallel lines; anterior region of prosternum with glandular ducts; antennal grooves absent. Procoxal cavity externally closed. Mesepimeron with pit. Mesosternum without parallel lines; glandular duct not opening onto a callus. Width of mesosternal process 2/3 that of mesocoxa. Metasternum with median longitudinal line. Ventrite 1 with 2 discal glandular ducts; meta-intercoxal process about as long as wide; metasubcoxal line absent. Ventrites with lateral glandular ducts, present on 1-5. Abdominal spiracles absent from segments 6 and 7. Prescutum with variolate microsculpture. Scutellum transverse. Epipleuron present to level of posterior margin of the metasternum. Hind wing present or absent; marginal setae present to level of RA+ScP vein; basal binding patch well or poorly developed; veins MP_3 and MP_4+CuA_1 absent. Tarsal formula 555; tarsomeres slightly lobed.

Female.— Body broader than that of males in some species (Johnson 1973). Spermatheca c-shaped; spermathecal duct unsclerotized or sclerotized, not coiled.

Male.— Body narrower than that of females in some species (Johnson 1973). Orientation of aedeagus horizontal in body. Spiculum gastrale symmetrical, broad. Tarsomeres 1-3 of pro- and mesotarsi dilated.

Diet.— Fungal spores and hyphae, some species are phytophagous (Newton 1932, Hinton 1945).

Habitat.— Rotting vegetation, dead wood, large mammal dung, mammal nests (Johnson 1993).

Larval descriptions.— *Atomaria linearis* Stephens (Newton 1932), *A. lewisi* (Lawrence 1991), *A. longipennis* (Casey) (Lawrence 1991), *A. nigripennis* (Erichson 1846), *A. ruficornis* (Marsham) (Evans 1961a).

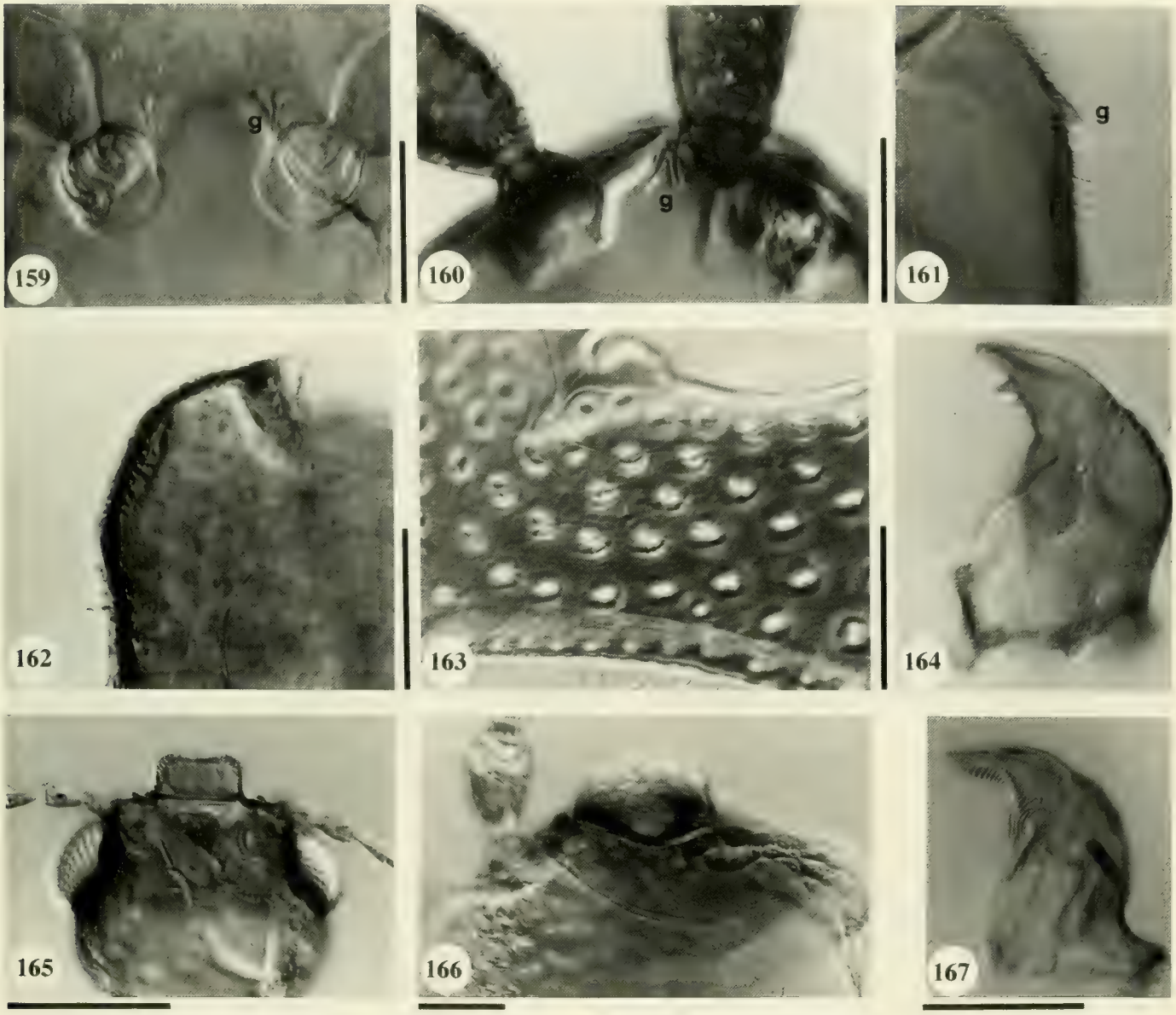
Distribution.— Holarctic, Africa, world wide (some species).

Discussion.— Although the genus *Atomaria* was described by Stephens (1830:64), Stephens (1829b) lists 28 species as members of the genus in the earlier published catalogue.

The genus *Atomaria* contains about 200 species. Major works include Casey (1900; North America), Johnson (1992; middle Europe), Johnson (1970, 1975b; Madeira and Canary Islands), Johnson (1973, *A. gibbula* group of Europe), and Sjöberg (1947, Europe). While the European fauna has been studied by C. Johnson, taxonomic works are unavailable for those species occurring in North America. A taxonomic revision for North America would be useful.

Wollaston (1854) described *Ephistemus alternans* and placed it in the subgenus *Microum.* Wollaston (1857) subsequently transferred *E. alternans* to *Atomaria,* although Reitter (1887) put it back into *Ephistemus* and Schenkling (1923) and others have it listed as a member of *Ootypus.* Although the species *A. alternans* is convex and broad-bodied, it is clearly a member of *Atomaria* (Johnson 1970).

Two subgenera that sometimes have been used as genera (e.g., Casey 1900 and Arnett 1969) *Anchicera* Thomson 1863 and *Atomaria* (= *Agathengis* as implemented by Casey 1900), have been consistently used for dividing *Atomaria.* Members of *Anchicera* tend to have a body form that is short and oval and the antennal insertions are somewhat separate. In contrast, members of *Atomaria*



Figs. 159-167. Morphological features of Cryptophagidae. **159,** *Ootypus globosus*, anterior view of head. **160,** *Salltius ruficeps*, anterior view of head. **161,** *Cryptogasterus lawrencei*, pronotal angularity. **162,** *Cryptophagus* nr. *tasmanicus*, pronotal angularity. **163,** *Cryptophagus* nr. *micramboides* (Asia), prosternum of male. **164,** *Atomaria* sp. (North America), dorsal view of right mandible. **165,** *Anitamaria* sp. (eastern Australia), dorsal view of head. **166,** *Mnioticus gibbinsi*, dorsal view of head showing glandular duct. **167,** *Caenoscelis* sp. (North America), ventral view of left mandible. (Scale bar = 0.1 mm, g = glandular duct).

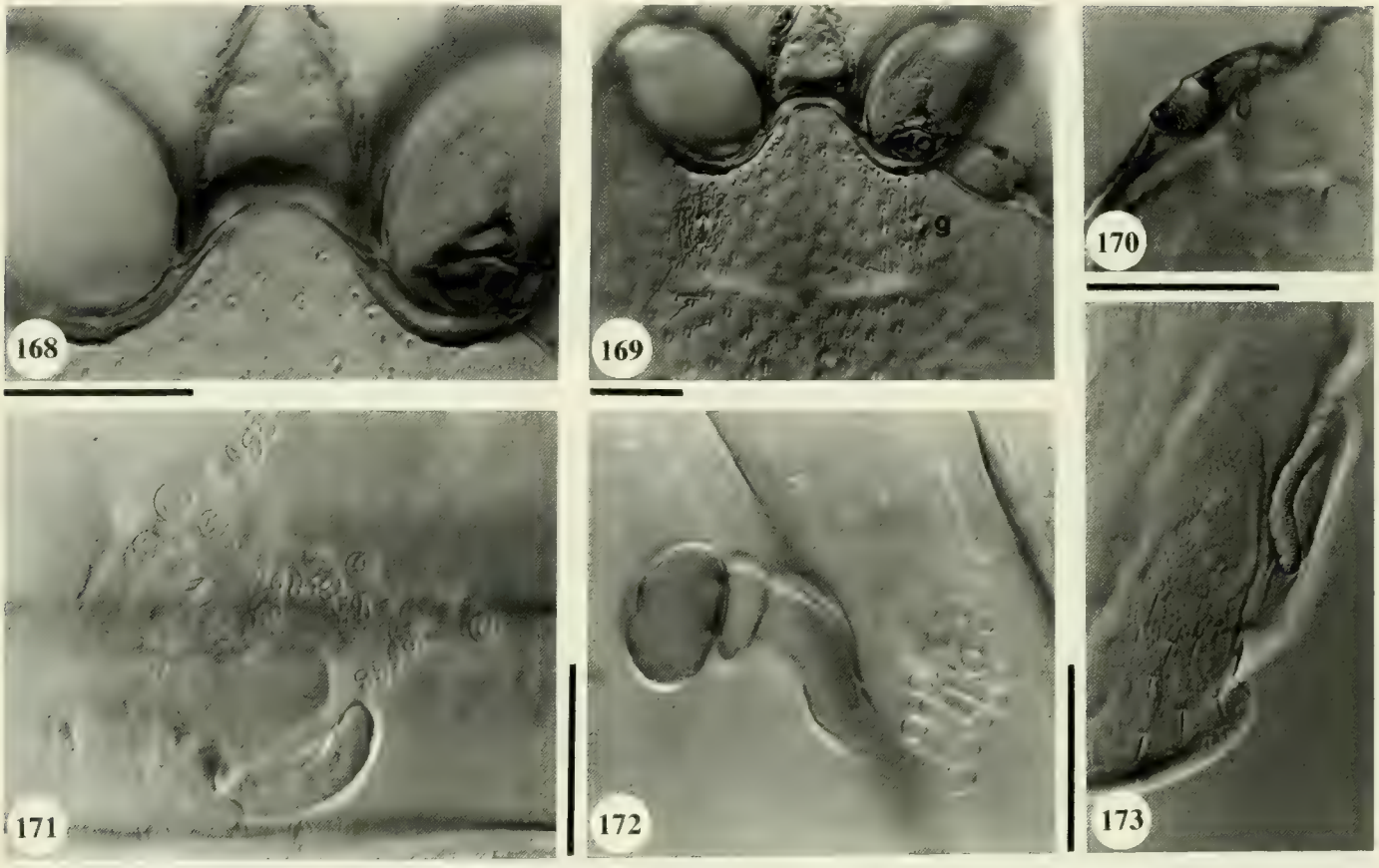
tend to have elongate bodies that are more parallel-sided and the antennal insertions are somewhat approximate. External examination of many species suggests that these diagnostic characters represent a grade of continuous variation of shape and length, and I have been unable to recognize any internal characters that support these subgenera (comparisons made of aedeagal characters were based also on drawings provided in C. Johnson's papers). A morphometric study of the subgenera may show that the variation among these characters is not continuous, thereby supporting the utility of these taxonomic categories.

Atomaria is placed phylogenetically as sister taxon to a clade containing south temperate species.

Genus *Atomaroides* Ljubarsky
(Fig. 55)

Atomaroides Ljubarsky, 1989:51. Type species: *Atomaria ussurica* Ljubarsky, 1987b, by monotypy.

Diagnosis.— Body form elongate; pronotum more or less parallel-sided, greatest width at middle. Antennal club 3-segmented. Cephalic glandular ducts not fused in middle. Antennal grooves on head and prosternum absent. Pronotum with lateral marginal bead wide. Prosternum without parallel lines; anterior glands present. Mesosternal glands not opening onto callus. Metasubcoxal lines absent. Tarsal formula 444; tarsomeres not strongly lobed.



Figs. 168-173. Morphological features of Cryptophagidae. **168,** *Anitamaria* sp. (eastern Australia), mesometasternal junction. **169,** *Anitamaria* sp. (Australia), meso- and metasternum (g = glandular duct pore). **170,** *Cryptophagus* nr. *tasmanicus*, abdominal spiracle on tergite 7. **171,** *Chilatomaria hillersae*, spermatheca and duct. **172,** *Salltius ruficeps*, spermatheca and duct. **173,** *Cryptophagus gibbipennis*, abdominal spiracle on tergite 7. (Scale bar = 0.1 mm).

Description.— Length 1.2-1.3 mm. Color of body dark brown. Body form more or less parallel-sided; oval-elongate. Body setae short, decumbent. Prosternal area with punctation. Head not constricted behind eye; boss on front of head absent; clypeus on same level as that of frons; antennal grooves absent; cephalic glandular ducts present not joined in middle. Antenna with 3-segmented club; antennomere 11 subequal to that of 10; antennomere 3 up to 2x the length of 4; shape of funicle conical and curved. Mandible without dorsal tubercles; basal sensory pores absent. Mentum with median process; transverse line or ridge absent. Eye prominent; ocular setae present. Pronotum parallel-sided, greatest width at middle; marginal bead wide. Hypomeron with notch near procoxal cavity. Prosternal process without parallel lines; anterior region of prosternum with glandular ducts. Procoxal cavity externally closed. Mesepimeron without pit. Mesosternum with parallel lines; glandular ducts not opening onto a callus. Width of mesosternal process 2/3 that of mesocoxa. Metasternum with median longitudinal line. Ventrite 1 without discal gland; meta-intercoxal process about as long as wide; metasubcoxal line absent. Ventrites with lateral glandular ducts, present on 1-4. Abdominal spiracles absent from segments 5 - 7. Prescutum with variolate microsculpture. Scutellum transverse. Epipleuron present at level of posterior margin of metasternum. Hind wing present; marginal setae present to level of RA+ScP vein; basal binding patch poorly developed; veins MP_3, MP_4+CuA_1, CuA_{3+4}, CuA_{3+4}+AA_{1+2} absent. Tarsal formula 444; tarsomeres slightly lobed.

Female.— Not examined.

Male.—Orientation of aedeagus horizontal in body. Spiculum gastrale symmetrical, broad. Tarsomeres 1-2 of pro- and mesotarsi dilated.

Distribution.— Eastern Russia.

Discussion.— The genus *Atomaroides* is monotypic. *Atomaroides ussurica* is unusual among members of Atomariinae because of the presence of a thickened lateral marginal bead on the pronotum and it is phylogenetically placed at the base of Atomariini.

Chilatomaria Leschen, new genus

(Figs. 19, 24, 37, 63, 65, 75, 112, 131, 152, 171, 198, 204)

Type species: *Chilatomaria hillersae* Leschen, new species

Diagnosis.— Body form elongate; pronotum more or less parallel-sided, greatest width at middle. Antennal club 3-segmented. Cephalic glandular ducts not fused in middle. Antennal grooves on head and prosternum absent. Pronotum with lateral marginal bead narrow. Prosternum without parallel lines; anterior glands present. Mesosternal glands opening onto a callus or not. Metasubcoxal lines present or absent. Tarsal formula 555; not strongly lobed.

Description.— Length 1.6-2.1 mm. Color of body light or dark brown, black, or bicolored. Body form parallel-sided, short or elongate. Body setae apressed, decumbent, short or long. Prosternal area with punctation. Head not constricted behind eye; boss on front of head absent; clypeus on same or lower plane as frons; antennal grooves absent; cephalic glandular ducts not fused at middle. Antenna with 3-segmented club; antennomere 11 subequal

to that of 10; antennomere 3 up to 2x the length of 4; shape of funicle conical and curved or not. Mandible with 2 dorsal tubercles; basal sensory pores present. Mentum with median process; transverse line or ridge present. Eye prominent; ocular setae present or absent. Pronotum parallel-sided, greatest width at middle; lateral marginal bead narrow. Hypomeron with or without notch near procoxal cavity. Prosternal process without parallel lines; anterior region of prosternum without glandular ducts; antennal grooves absent. Procoxal cavity externally closed. Mesepimeron with pit. Mesosternum with procoxal rests; parallel lines present or absent; glandular duct present, callus present or not. Width of mesosternal process 2/3 that of mesocoxa. Metasternum with median longitudinal line. Ventrite 1 with 2 discal glandular ducts; meta-intercoxal process about as long as wide; metasubcoxal line present or absent. Ventrites with lateral glandular ducts, present on 1-5. Abdominal spiracles absent from segment 7 or 6 and 7. Prescutum with variolate microsculpture. Scutellum transverse. Epipleuron present to level of posterior margin of metasternum. Hind wing present or not; marginal setae present to level of RA+ScP vein; basal binding patch present; vein MP_3 absent. Tarsal formula 555; tarsomeres slightly or not lobed.

Female.— Spermatheca c-shaped; spermathecal duct sclerotized or not, coiled or not.

Male.— Orientation of aedeagus horizontal. Spiculum gastrale of male symmetrical, broad. Tarsomeres 1-3 of pro- and mesotarsi dilated.

Diet.— Fungal spores and hyphae, pollen (personal observation).

Habitat.— Leaf litter, vegetation.

Distribution.— Australia, South America.

Discussion.— The genus *Chilatomaria* is proposed for several species found in the south temperate regions. Although there is extensive variation in the genus, members that are similar to *Atomaria australis* Blackburn and *Atomaria lindensis* Blackburn, that are strongly punctate and areolate, are consistently placed as sister taxa to another group containing species that are more or less glabrous (*Chilatomaria* group). Whether these two groups of species actually correspond to monophyletic groups requires that all species be described and included in a cladistic analysis. In this work I place these species into one genus; therefore those species described by Blackburn (1891) are new combinations in *Chilatomaria*.

Etymology.— The generic name is derived from the name of the country Chile and the root word *Atomaria*, a genus that the type species closely resembles.

Chilatomaria hillersae Leschen, new species
(Figs. 19, 24, 63, 75, 112, 131, 152, 171, 198)

Description.— Length 1.35-1.70 mm (n = 10). Color of body dark or charcoal brown; elytron with humerus and apex yellow or yellow brown; mouthparts and legs light brown. Punctation dense, average width of puncture 0.001 mm; microscultpure not areolate throughout body. Body setae short, decumbent; average length 0.002. Head sparsely punctate, punctures separated by about 1.5 diameter; interantennal distance = 0.014 mm; clypeus on same plane as frons. Eye prominent; finely faceted; ocular setae present. Antenna elongate, extending to basal 1/3 of pronotum; antennomere relative lengths 9:8:6:5:5:4:4:4:5:6:8; funicle not curved or conical. Pronotum about 0.73 x as long as wide (PL/MPW = 0.66 - 0.74 , x = 0.74); depth = 0.34 - 0.40, x = 0.36 mm; notch above procoxal cavity absent; punctures of disk separated by about 1/2 - 1 diameter; areolate microsculpture distributed at base. Margin of prothorax emarginate; anterior angles of prothorax acute. Prosternum with areolate microsculpture; prosternal process shorter than anterior portion, lateral margins arcuate, posterior margin slightly concave. Elytra about 1.50 x as long as wide (EL/MEW = 1.38 - 2.07, x = 1.50) and 2.68 x as long as pronotum (EL/PL = 2.42 - 2.90, x = 2.68); punctures separated by 2 diameters. Mesosternum without deep pits; parallel lines present. Mesepimeron with a deep pit, containing 3 setae. Metasternal process evenly arcuate; submetacoxal lines parallel and in contact with discal glandular duct pores. Hind wing present. Spiracles absent from segments 6 and 7. Spermatheca sclerotized, coiled. Aedeagus as in Fig. 112.

Diet.— Fungal spores and hyphae (personal observation).

Habitat.— Leaf litter.

Discussion.— *Chilatomaria hillersae* can be distinguished from other species of *Chilatomaria* by the acute anterior angles of the prothorax, absence of areolate microsculpture from most of the body and the yellow color of the humerus and apex of the elytron.

Etymology.— Named in honor of R. Hillers, Graduate Division Office at the University of Kansas.

Type.—Holotype, with labels as follows, "Chile: Palena Prov, 37 km SE Chaiten, 28.XII.84 - 30.I.85, S & J Peck, FIT, 60 m riverside 2nd forest, HOLOTYPE *Chilatomaria hillersae* R. Leschen 1994" (CNIS).

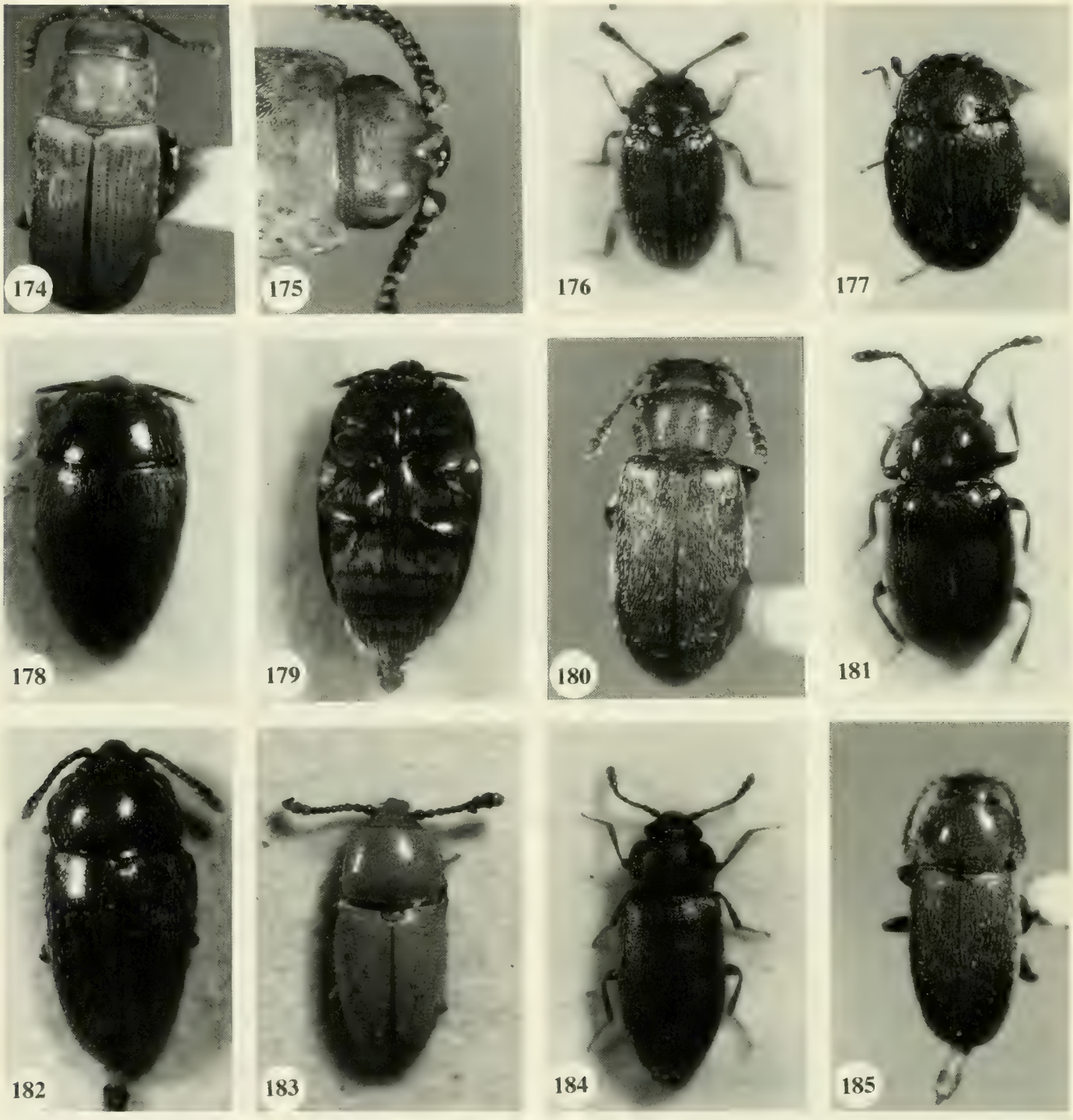
Paratypes.—40. CHILE: AISEN. 1, Cisnes to Las Juntas, 30.xii.84, S & J Peck, forest and pasture car netting (CMN). CAUTIN. 1, 1.5 mi NW Nueva Imperial, Chacamo, 18 - 23.II.1981, FMHD #81-148, ex *Nothof. dombey* litter, L. Peña. (FMNH). LLANQUIHUE. 4, (1 on microslide), Lago Chapo, 34 km E Pto. Mont, 24.XII.84 - 2.II.85, S & J Peck, 300m, FIT 2nd growth *Nothofagus* (CMN); 2, Lenca, 45 km SE Pto Mont, 100m, 25.XII.1984, FMHD #85-947, forest remnant, leaf stick litter, S & J Peck, P#85-63, Berlese (FMNH). MALLECO. 2, Puren Contulmo Natur. Mon. 11.XII.84- 13.II.85, S & J Peck, FIT, 350m, mixed evergr. forest. (CMN); 3, 40 km W Angol, Nahuelbuta Nat. Pk. 9.XII.84 - 17.II.85, S & J Peck, 12-1500 m, FITs, *Nothofagus Auracaria* forest (CMN). OSORNO. 10, Puyehue Nat. Pk, Aguas Calientes, 20.XII.84 - 8.II.85, S & J Peck, 500 m, FIT, Derumbes Forest Trail (ANIC, CMN, MANC, MNHG); 7, same except 18.XII.84 - 8.II.85, 600 m, malaise, *Nothophagus* forest (ANIC, CMN, SEMC); 1, 13 km W Entre Lagos, 21.XII.84 - 8.II.85, S & J Peck, 200m, cartp. forest remnant (CMN); 1, 3 km S Maicolpue, Bahia Mansa, 21.XII.84 - 3.II.85, S & J Peck, 200m, cartp. mixed forest (CMN). VALDIVIA. 8, (1 on microslide) 34 km WNW La Union, 17.XII.84 - 7.II.85, S & J Peck, 700m, FIT mixed evergr. forest (CMN, RALC)

Genus *Curelius* Casey

Curelius Casey, 1900:127. Type species: *Ephistemus dilutus* Reitter, 1883, here designated.

Diagnosis.— Body form round and convex; pronotal sides converging anteriorly, greatest width at base. Antennal club 3-segmented. Cephalic glandular ducts not fused in middle. Antennal grooves on head and prosternum absent. Pronotum with lateral marginal bead narrow. Prosternum with parallel lines; anterior glands present. Mesosternal glands not opening onto a callus. Metasubcoxal lines absent. Tarsal formula 555; tarsomeres slightly lobed.

Description.— Length 0.8-1.0 mm. Color of body yellow, light or dark brown. Body form convex, oval. Body setae sparse, suberect. Prosternal area without punctation. Head not constricted behind eye; boss on front of head absent; clypeus on same level as that of frons; antennal grooves absent; cephalic glandular ducts not fused in middle. Antenna with 3-segmented club; antennomere 11 subequal to that of 10; antennomere 3 up to 3x the length of 4; shape of funicle conical and curved. Mandible with 1 dorsal tubercle; basal sensory pores present. Mentum with median process; transverse line or ridge absent. Eye prominent; ocular setae present. Pronotum with sides converging anteriorly, greatest width at base; marginal bead narrow. Hypomeron with notch near procoxal cavity. Prosternal process with parallel lines; anterior region of prosternum with glandular ducts. Procoxal cavity externally open. Mesepimeron without pit. Mesosternum with parallel lines; glandular ducts not opening onto a callus. Width of mesosternal process greater than that of mesocoxa. Metasternum without median longitudinal line. Ventrite 1 with 2 discal



Figs. 174-185. Dorsal views of Cryptophagidae (L = length of beetles given in mm). **174,** *Antherophagus* sp. (North America) (L = 3.90). **175,** Same. **176,** *Henotiderus lorna* (L = 1.91). **177,** *Asternodea loebli* (holotype) (L= 1.23). **178,** *Catopochrotus crematogastri* (L = 2.44). **179,** Same, ventral view (L = 2.05). **180,** *Cryptophagus acutangulus* (L = 2.12). **181,** *Henoticus* sp. (Nepal) (L = 2.13). **182,** *Spantophaenus caucasicus* (paratype) (L = 2.44). **183,** *Mnionomidius serricollis* (paratype) (L = 2.06). **184,** *Micrambe abietis* (L = 2.56). **185,** *Mnioticus hancocki* (L = 3.19).

glandular ducts; meta-intercoxal process wider than long; meta-subcoxal line absent. Ventrites with lateral glandular ducts, present on 1-5. Abdominal spiracles absent from segments 6 and 7. Prescutum with variolate microsculpture. Scutellum weakly transverse. Epipleuron present to level of posterior margin of the metasternum. Hind wing present; marginal setae present to level of RA+ScP vein; basal binding patch poorly developed; vein MP_3, MP_4+CuA_1, and CuA_{3+4} absent. Tarsal formula 555;

tarsomeres slightly lobed.

Female.— Spermatheca c-shaped; spermathecal duct not sclerotized.

Male.— Orientation of aedeagus horizontal in body. Spiculum gastrale symmetrical, broad. Tarsomeres 1-3 of pro- and mesotarsi dilated.

Diet.— Fungal spores and hyphae (personal observation).

Habitat.— Rotting vegetation (unpublished data).

Distribution.— Mainly circumtropical, introduced to southern United States.

Discussion.— The genus *Curelius* contains three species. Johnson (1971) reviewed the taxonomic status and the Palaearctic species of *Curelius*.

Curelius is placed in a monophyletic group containing *Tisactia* and *Ephistemus*. *Curelius* appears more similar to *Ephistemus* based on overall body shape and can be distinguished from it by the absence of antennal grooves.

Genus *Ephistemus* Stephens
(Figs. 126, 149)

Ephistemus Stephens, 1829a:167. Type species: *Dermestes gyrinoides* Marsham, 1802, by subsequent designation (Westwood 1840:10).

Diagnosis.— Body form round and convex; pronotal sides converging anteriorly, greatest width at base. Antennal club 3-segmented. Cephalic glandular ducts not fused in middle. Antennal grooves on head and prosternum present. Pronotum with lateral marginal bead narrow. Prosternum with parallel lines; anterior glands present. Mesosternal glands not opening onto callus. Metasubcoxal lines absent. Tarsal formula 555; tarsomeres slightly lobed.

Description.— Length 0.9-1.4 mm. Color of body light or dark brown, black, elytron bicolored in 1 species. Body form round, convex. Body setae sparse, short. Prosternal area without punctation. Head not constricted behind eye; boss on front of head absent; clypeus on same or lower plane than that of frons; antennal grooves absent; cephalic glandular ducts present, not fused at middle. Antenna with 3-segmented club; antennomere 11 subequal to that of 10; antennomere 3 up to 3x the length of 4; shape of funicle conical and curved. Mandible with or without 1 dorsal tubercle; basal sensory pores present. Mentum with median process; transverse line or ridge absent. Eye prominent; ocular setae present. Pronotum with sides converging anteriorly, greatest width at base; lateral marginal bead narrow. Hypomeron with notch near procoxal cavity. Prosternal process with parallel lines; anterior region of prosternum with glandular ducts; antennal grooves present. Procoxal cavity externally open. Mesepimeron without pit. Mesosternum with parallel lines; glandular ducts not opening onto a callus. Width of mesosternal process greater than mesocoxa. Metasternum without median longitudinal line. Ventrite 1 with 2 discal glandular ducts; meta-intercoxal process wider than long; metasubcoxal line absent. Ventrites with lateral glandular ducts, present on 1-5. Abdominal spiracles absent from segments 6 and 7. Prescutum with variolate microsculpture. Scutellum weakly transverse. Epipleuron present to level of posterior margin of metasternum. Hind wing present; marginal setae present to level of RA+ScP vein; basal binding patch poorly developed; vein MP_3, MP_4+CuA_1, and CuA_{3+4} absent. Tarsal formula 555; tarsomeres slightly lobed.

Female.— Spermatheca c-shaped; spermathecal duct unsclerotized.

Male.— Orientation of aedeagus horizontal. Spiculum gastrale of male symmetrical, broad. Tarsomeres 1-3 of pro- and mesotarsi dilated.

Diet.— Fungal spores and hyphae (personal observation).

Habitat.— Rotting vegetation, mammal dung, ant nests (C. Johnson personal communication).

Distribution.— Holarctic, circumtropical.

Discussion.— The genus *Ephistemus* contains six described species; however, there are undescribed forms in Central and South America.

Ephistemus is placed in a monophyletic group containing the genera *Tisactia* and *Curelius*. *Ephistemus* is most similar to members of *Curelius* which also have an oval body form but lack antennal grooves on the head and prosternum.

Genus *Microatomaria* Leschen, new genus
(Figs. 27, 59, 77, 98, 105, 205)

Type species: *Microatomaria hintoni* Leschen, new species

Diagnosis.— Body form elongate; pronotum more or less parallel-sided, greatest width at middle. Antennal club 2-segmented. Cephalic glandular ducts not fused in middle. Antennal grooves on head and prosternum absent. Pronotum with lateral marginal bead narrow. Prosternum with parallel lines; anterior glands absent. Mesosternal glands opening onto a callus. Metasubcoxal lines absent. Tarsal formula 555; tarsomeres slightly lobed.

Description.— Length 0.9-1.1 mm. Color of body light brown. Body form short, parallel-sided. Body setae short, decumbent. Prosternal area with punctation. Head not constricted behind eye; boss on front of head absent; clypeus on same level as that of frons; antennal grooves absent; cephalic glandular ducts not fused in middle. Eye prominent; ocular setae present. Antenna with 2-segmented club; antennomere 11 subequal to that of 10; antennomere 3 up to 2x the length of 4; shape of funicle not conical or curved. Mandible with 2 dorsal tubercles; basal sensory pores present. Mentum with median process; transverse line or ridge absent. Pronotum parallel-sided, greatest width at middle; lateral marginal bead narrow. Hypomeron without notch near procoxal cavity. Prosternal process without parallel lines; anterior region without glandular ducts; antennal grooves absent. Procoxal cavity externally closed. Mesepimeron with pit. Mesosternum with parallel lines; glandular ducts present, opening onto a callus. Width of mesosternal process equal to that of mesocoxa. Metasternum without a median longitudinal line. Ventrite 1 with 2 discal glandular ducts; meta-intercoxal process about as long as wide; metasubcoxal line present. Ventrites with lateral glandular ducts, present on 1-5. Abdominal spiracles present on segments 1-7. Prescutum with variolate microsculpture. Scutellum transverse. Epipleuron present to level of posterior margin of metasternum. Hind wing present; marginal setae present to level of RA+ScP vein; basal binding patch present; veins MP_3, MP_4+CuA_1, CuA_{3+4}, CuA_{3+4}+AA_{1+2} absent. Tarsal formula 555; tarsomeres slightly lobed.

Female.— Spermatheca c-shaped; spermathecal duct sclerotized, not coiled.

Male.— Orientation of aedeagus horizontal. Spiculum gastrale symmetrical, broad. Tarsomeres 1-3 of pro- and mesotarsi dilated.

Diet.— Fungal spores and hyphae (personal observation).

Habitat.— Leaf litter.

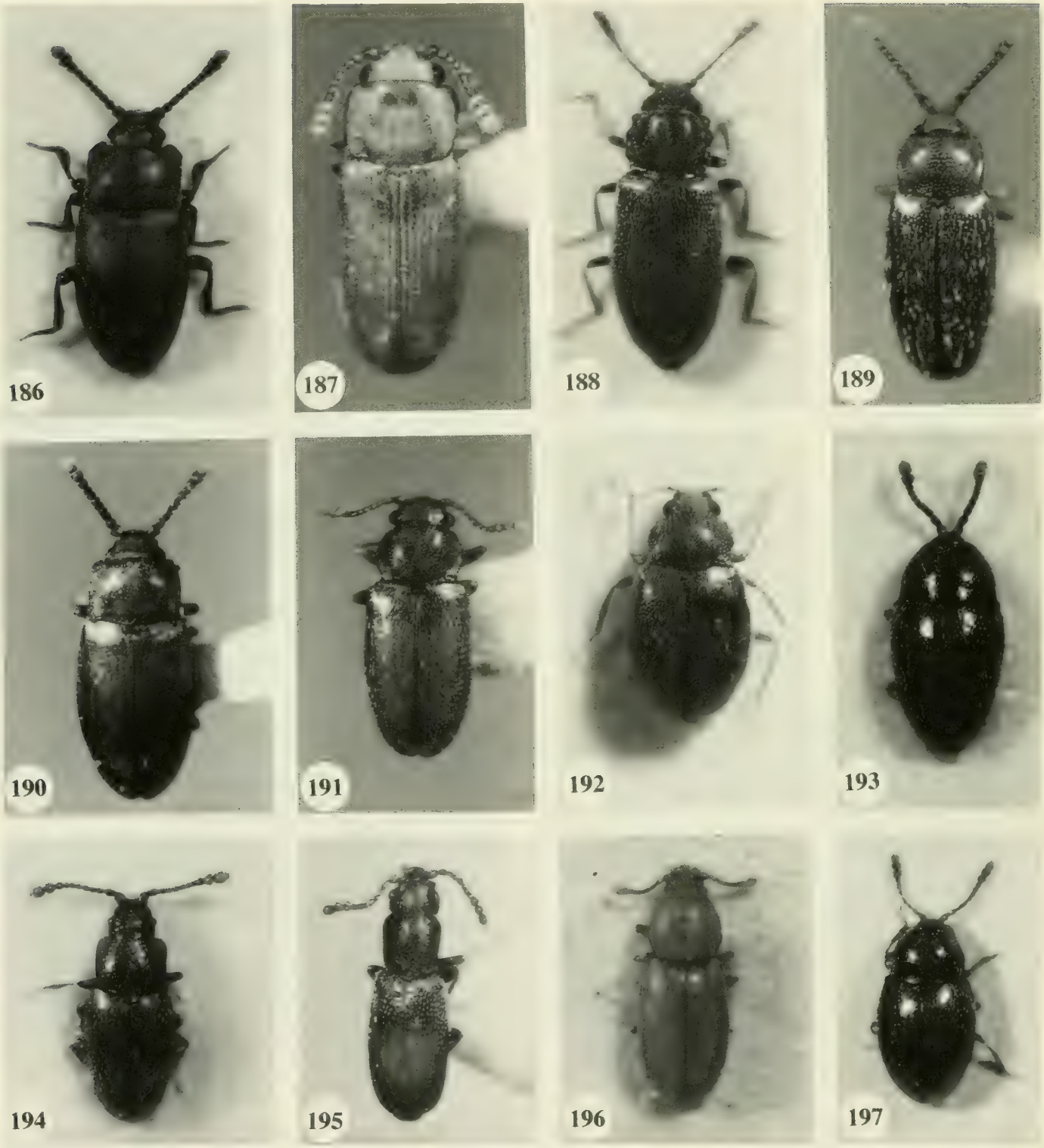
Distribution.— Northeastern Australia, New Guinea.

Discussion.— The genus *Microatomaria* is described for one species among Atomariini that has a 2-segmented antennal club, an unusual feature among Atomariini. *Microatomaria* is a member of the south temperate Atomariini.

Etymology.— The generic name is derived from the root word *Atomaria*, a genus that the type species resembles, and the Greek word mikros, meaning small.

Microatomaria hintoni Leschen, new species
(Figs. 27, 59, 77, 98, 105, 205)

Description.— Length 0.89-1.08 mm (n = 10). Color of body light brown. Punctation dense, average width of puncture 0.001 mm; separated by 1 diameter. Body setae short, decumbent; average length 0.003 mm. Head densely punctate; areolate microsculpture present at dorsal base and venter; interantennal distance = 0.011 mm. Eye prominent; coarsely faceted. Antenna elongate, extending to basal 1/3 of pronotum; antennomere relative lengths 5:5:4:3:3:3:3:3:3:4:4:4. Pronotum about 0.62 x as long as wide (PL/MPW = 0.52 - 0.68 , x = 0.68); depth = 0.32 - 0.39, x = 0.35 mm.



Figs. 186-197. Dorsal views of Cryptophagidae (L = length of beetles given in mm). **186,** *Spavius glaber* (L = 2.44). **187,** *Pteryngium crenatum* (L = 1.79). **188,** *Salebius* sp. (L = 2.08). **189,** *Caenoscelis* sp. (North America) (L = 2.00). **190,** *Myrmedophila americana* (L = 2.22). **191,** *Neohenoticus palmerae* (holotype) (L = 1.60). **192,** *Serratomaria vulgaris* (paratype) (L = 1.76). **193,** *Sternodea baudii* (L = 1.36 mm). **194,** *Neopicrotus peckorum* (paratype) (L = 1.22). **195,** *Hypocoprus tenuis* (L = 1.12). **196,** *Alfieriella denticulata* (L = 1.02). **197,** *Atomaria gibbula* (L = 1.61).

Prosternal process shorter than anterior portion of prosternum; posterior margin with sides notched. Elytra about 1.30 x as long as wide (EL/MEW = 1.26 - 1.38, x = 1.30) and 2.48 x as long as pronotum (EL/PL = 2.20 - 2.98, x = 2.48). Mesepimeron with a small pit, containing 1-3 setae. Metasternal process evenly quadrate. Aedeagus as in Fig. 105.

Etymology.— Named in honor of H. E. Hinton, a distinguished insect systematist and biologist.

Type.—Holotype, with labels as follows, "15.47S 145.14E Shiptons Flat QLD 17-19 Oct. 1980 T. Weir, Berlesate ANIC 697 Sieved rain forest litter, HOLOTYPE *Microatomaria hintoni* R. Leschen 1994" (ANIC).

Paratypes.— 12. AUSTRALIA: QUEENSLAND. 1, same as holotype except 16-18 May 1981, A. Calder & J. Feehan (ANIC 738) (ANIC); 2, 16.08S 145.26E Noah Ck., 7km ENE Thornton Peak, 27 Mar. 1984, A. Calder & T. Weir, Berlesate ANIC 946, lowland rainforest (ANIC); 7, (2 slide mounted) 16.03S to 16.05S 145.28E, Cape Tribulation area, 21-28 Mar. 1984, A. Calder & T. Weir, Berlesate, ANIC 944, Rainforest on steep slope (ANIC, RALC, MANC). NEW GUINEA: 2, SE Port Moresby, Brown River, 17-18.VIII.1968, No. NG-P.R.l, leg Dr. I Loksa (HUNG).

Genus *Ootypus* Ganglbauer
(Figs. 159, 208)

Ootypus Ganglbauer, 1899:737. Type species: *Ephistemus globosus* Waltl, 1838, by monotypy.

Diagnosis.— Body form round, convex; pronotal sides converging anteriorly, greatest width at base. Antennal club 3-segmented. Cephalic glandular ducts not fused in middle. Antennal grooves on head and prosternum absent. Pronotum with lateral marginal bead narrow. Prosternum without parallel lines; anterior glands present. Mesosternal glands not opening onto callus. Metasubcoxal lines absent. Tarsal formula 555; tarsomeres slightly lobed.

Description.— Length 1.7-2.1 mm. Color of body dark brown; elytron with reddish brown apex. Body form round, convex. Body setae sparse, short, apressed. Prosternal area without punctation. Head not constricted behind eye; boss on front of head present; clypeus on lower plane than that of frons; antennal grooves absent; cephalic glandular ducts not fused at middle. Eye prominent; ocular setae present. Antenna with 3-segmented club; antennomere 11 subequal to that of penultimate antennomere 10; antennomere 3 up to 2x the length of 4; shape of funicle conical and curved. Mandible with 2 dorsal tubercles; basal sensory pores present. Mentum with median process; transverse line or ridge absent. Pronotum with sides converging anteriorly, greatest width at base; marginal bead narrow. Hypomeron with notch near procoxal cavity. Prosternal process without parallel lines; anterior region of prosternum with glandular ducts; antennal grooves absent. Procoxal cavity externally open. Mesepimeron without pit. Mesosternum without parallel lines; glandular ducts present. Width of mesosternal process equal to that of mesocoxa. Metasternum without median longitudinal line. Ventrite 1 with 2 discal glandular ducts; meta-intercoxal process about as long as wide; metasubcoxal line absent. Ventrites with lateral glandular ducts, present on 1-5. Abdominal spiracles absent from segments 6 and 7. Prescutum with variolate microsculpture. Scutellum weakly transverse. Epipleuron present to level of posterior margin of metasternum. Hind wing present; marginal setae present to level of RA+ScP vein; basal binding patch poorly developed; veins MP_3, MP_4+CuA_1, and CuA_{3+4} absent. Tarsal formula 555; tarsomeres slightly lobed.

Female.— Spermatheca c-shaped; spermathecal duct unsclerotized.

Male.—Orientation of aedeagus horizontal. Spiculum gastrale symmetrical, broad. Tarsomeres 1-3 of pro- and mesotarsi dilated.

Diet.— Fungal spores and hyphae (personal observation).

Habitat.— Large mammal dung (Johnson 1993).

Distribution.— Palearctic, northern Africa.

Discussion.— The genus *Ootypus* is monotypic and is sister taxon to *Ephistemus* and its relatives.

Paratomaria Leschen, new genus
(Figs. 30, 56, 113, 154, 199)

Type species: *Paratomaria crowsoni* Leschen, new species

Diagnosis.— Body form elongate; pronotum more or less parallel-sided, greatest width at middle. Antennal club 3-segmented. Cephalic glandular ducts not fused in middle. Antennal grooves on head and prosternum absent. Pronotum with lateral marginal bead narrow. Prosternum without parallel lines; anterior glands absent. Mesosternal glands not opening onto callus. Metasubcoxal lines present. Tarsal formula 555; tarsomeres strongly lobed.

Description.— Length 1.8-2.1 mm. Color of body light, dark, chocolate brown; elytron may be infuscate. Body form parallel-sided, elongate. Body setae long, apressed. Prosternal area with punctation. Head not constricted behind eye; boss on front of head present; clypeus on lower plane than that of frons; antennal grooves absent; cephalic glandular ducts not fused at middle. Eye prominent; ocular setae present. Antenna with 3-segmented club; antennomere 11 subequal to that of 10; antennomere 3 up to 2x the length of 4; shape of funicle conical and curved. Mandible with 2 dorsal tubercles; basal sensory pores present. Mentum with median process; transverse line or ridge present. Pronotum parallel-sided, greatest width at middle; marginal bead narrow. Hypomeron without a notch near procoxal cavity. Prosternal process without parallel lines; anterior region of prosternum without glandular ducts; antennal grooves absent. Procoxal cavity externally closed. Mesepimeron with pit. Mesosternum without parallel lines; glandular ducts not opening onto a callus. Width of mesosternal process 2/3 that of mesocoxa. Metasternum with median longitudinal line. Ventrite 1 with 2 discal glandular ducts; meta-intercoxal process about as long as wide; metasubcoxal line present. Ventrites with lateral glandular ducts, present on 1-5. Abdominal spiracles present on segments 1-7. Prescutum with variolate microsculpture. Scutellum transverse. Epipleuron present to level of posterior margin of metasternum. Hind wing present; marginal setae present to level of RA+ScP vein; basal binding patch present; veins MP_3 and CuA_{3+4} absent. Tarsal formula 555; tarsomeres distinctly lobed, tarsomere 3 dilated.

Female.— Spermatheca c-shaped; spermathecal duct unsclerotized.

Male.— Orientation of aedeagus horizontal in body. Spiculum gastrale symmetrical, broad.

Diet.— Pollen (personal observation).

Habitat.— Vegetation.

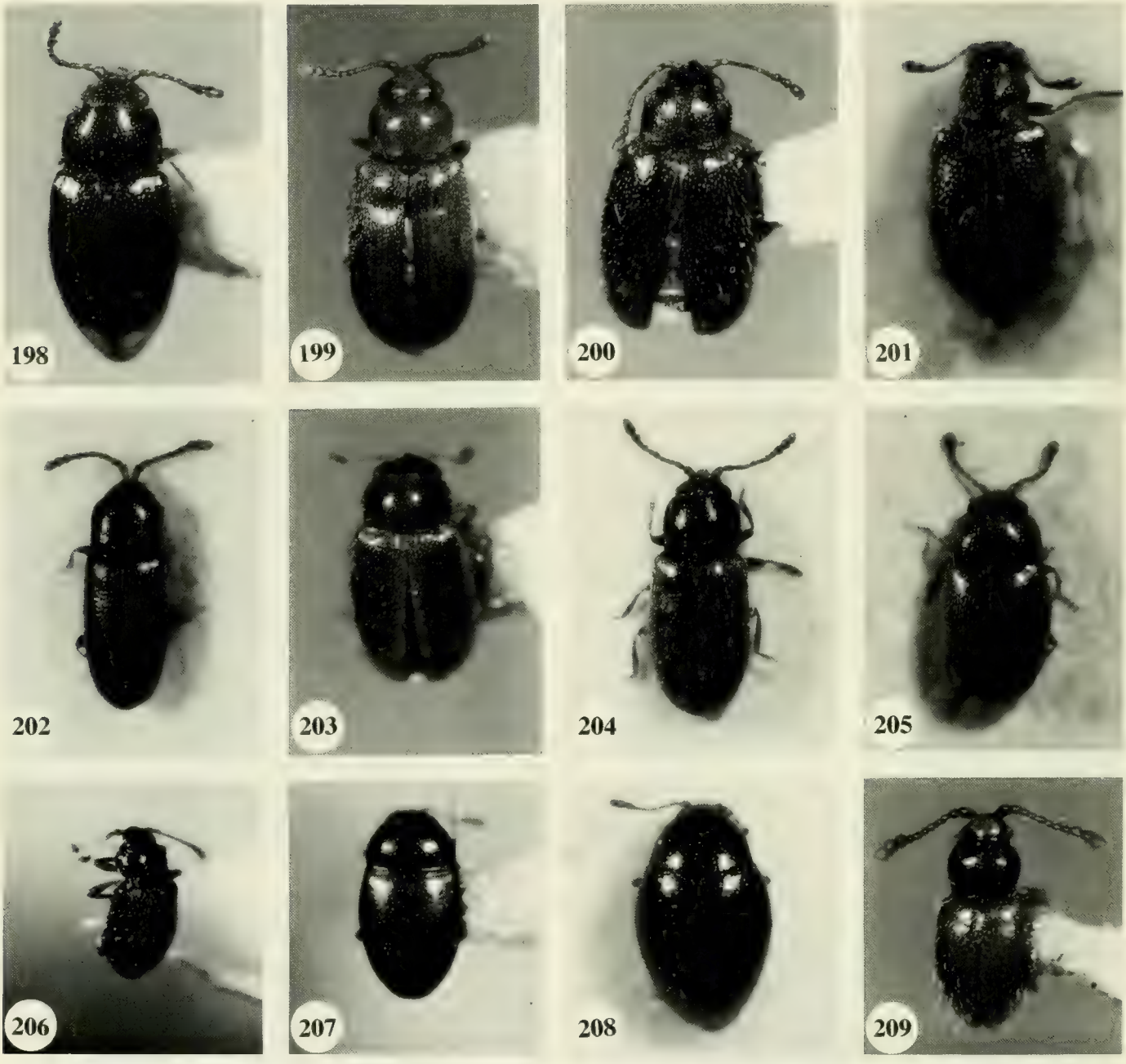
Distribution.— New Zealand.

Discussion.— The genus *Paratomaria* is described for a relatively abundant species of south temperate atomariine commonly collected on vegetation. *Paratomaria* is a basal member of the south temperate Atomariini.

Etymology.— The generic name is derived from the root word *Atomaria*, a genus that the type species closely resembles, and the Greek word para, meaning near.

Paratomaria crowsoni Leschen, new species
(Figs. 30, 56, 113, 154, 199)

Description.— Length 1.23-1.68 mm (n = 10). Color of body light or dark brown; elytron infuscate in some specimens. Punctation moderately dense, average width of puncture 0.001 mm. Body setae short, apressed; average length 0.031 mm. Head sparsely punctate, punctures separated by about 1 - 1.5 diameter; interantennal distance = 0.013 mm. Eye prominent; finely faceted. Antenna elongate, extending beyond base of pronotum; antennomere relative lengths 9:8:6:5:6:5:5:4:5:5:7. Pronotum gradually widened near anterior half; about 0.78 x as long as wide (PL/MPW = 0.70 - 0.85 , x = 0.78); depth = 0.29 - 0.36, x = 0.33 mm; punctures of disk separated by about 1/2 - 1 diameter. Prosternum with length of prosternal process 1/6 shorter than that of anterior portion. Elytra about 1.62 x as long as wide (EL/MEW = 1.38 - 2.07, x = 1.62) and 2.82 x as long as pronotum (EL/PL = 2.54 - 3.22, x =



Figs. 198-209. Dorsal views of Cryptophagidae (L = length of beetles given in mm). **198,** *Chilatomaria hillersae* (holotype) (L = 1.83). **199,** *Paratomaria crowsoni* (holotype) (L = 1.69). **200,** *Anitamaria thayerorum* (paratype) (L = 1.56). **201,** *Cryptafricus leleupi* (holotype) (L = 1.68). **202,** *Atomaria linearis* (L = 1.44). **203,** *Cryptogasterus lawrencei* (paratype) (L = 1.38). **204,** *Chilatomaria lindensis* (holotype) (L = 1.89). **205,** *Microatomaria hintoni* (paratype) (L = 1.04). **206,** *Microphagus johnsoni* (holotype) (L = 0.75). **207,** *Tisactia subglabra* (L = 1.68). **208,** *Ootypus globosus* (L = 1.65). **209,** *Salltius ruficeps* (L = 1.44).

2.82); punctures separated by 1 - 1.5 diameters. Mesepimeron with a pit, containing 1-2 setae. Metasternal process quadrate. Aedeagus as in Fig. 113.

Discussion.— There are many specimens of *Paratomaria* deposited in the collections at NZAC and BMNH and among this material there are specimens that differ in color (mainly darker) from the type series of *P. crowsoni.* Dissections of these variants may verify that they are conspecific with *P. crowsoni.*

Etymology.— Named in honor of R. A. Crowson, an authority on Coleoptera biology and systematics.

Type.—Holotype, with labels as follows, "New Zealand: Big S. Cape I, SW Stewart I, Nov. '68, J. C. Watt, *Dracophyllum longifolium,* (N.Z. Arthropod Coll. Entomology. DSIR, Auckland New Zealand), HOLOTYPE *Paratomaria crowsoni* designated by R. Leschen 1994" (NZAC).

Paratypes.— 146. NEW ZEALAND: 47, same as Holotype (NZAC); same as Holotype except: 3, Sweeping moor, 10 Feb. 1969, A. C. Eyles (NZAC); 41, General beating, Nov. 1968, G. Kuschel (NZAC, RALC, ANIC, SEMC, FMNH, MANC, PARI); 1, *Senecio,* 7 Feb. 1969, B. A. Kuschel (NZAC); 8, *Olearia conensoi* (dead twigs)

Nov. 1968, G. Kuschel (NZAC, PARI); 2, General beating, Feb. 1969, J. I. Townsend (NZAC); 3, Sweeping grass, weeds, Feb. 1969, A. C. Eyles (NZAC); 1, Sweeping ferns, Feb.1969, A. C. Eyles (NZAC); 17, Beating coastal forest, Nov. 1968, J. C. Watt (NZAC); 5, *Pseudopanax*, Feb.1969, B. A. Kuschel (NZAC); 1, Beating coastal trees, 13 Nov. 1968, J. C. Watt (NZAC); 2, Under weeds, 12 Feb. 1969, A. C. Eyles (NZAC); 1, Cape Pigeon, *Daphon capensis*, 20 Nov. 1968, J. S. Dugdale and J. C. Watt (NZAC); 1, *Hebe elliptica*, Nov. 1968, G. Kuschel (NZAC); 4, Litter, Nov. 1968, J. McBurney (NZAC); 1, Beating, Nov. 1968, A. C. Eyles (NZAC); 1, *Phormium colensoi*, Nov. 1968, G. Kuschel (NZAC); 1, Mat plants, 12 Nov. 1968, G. Kuschel (NZAC); 2, Coastal rocks, Nov.1968, J. Dugdale (NZAC); 2, In forest, Nov. 1968. A. C. Eyles (NZAC); 1, Stephens I, Beating and sweeping tussock, Feb. 1971, G. Ramsey (NZAC).

Genus *Salltius* Broun
(Figs. 160, 172, 209)

Salltius Broun, 1893:1347. Type species: *Cryptophagus ruficeps* Broun, 1880, by monotypy.

Diagnosis.— Body form elongate; slightly constricted at base of prothorax and base of elytra (more or less biconvex). Antennal club 3-segmented. Cephalic glandular ducts fused in middle. Antennal grooves on head and prosternum absent. Pronotum with lateral marginal bead narrow. Prosternum without parallel lines; anterior glands absent. Mesosternal glands opening onto callus. Metasubcoxal lines present. Tarsal formula 555; tarsomeres strongly lobed.

Description.— Length 1.5-1.8 mm. Color of body light or red brown. Body form elongate; slightly constricted at base of prothorax and base of elytra (more or less biconvex). Body setae biseriate, long and erect, short and decumbent. Prosternal area with punctation. Head constricted behind eye; boss on front of head present; clypeus on lower plane than that of frons; antennal grooves absent; cephalic glands fused at middle of head. Eye not prominent; ocular setae absent. Antenna with 3-segmented club; antennomere 11 subequal to that of 10; antennomere 3 up to 2x the length of 4; shape of funicle conical and curved. Mandible with 2 dorsal tubercles; basal sensory pores present. Mentum without a median process; transverse line or ridge absent. Pronotum parallel-sided, greatest width at middle; lateral marginal bead narrow. Hypomeron without a notch near procoxal cavity. Prosternal process without parallel lines; anterior region of prosternum without glandular duct; antennal grooves absent. Procoxal cavity externally closed. Mesepimeron with pit. Mesosternum with parallel lines; glandular ducts opening onto a callus. Width of mesosternal process 2/3 that of mesocoxa. Metasternum with or without longitudinal line. Ventrite 1 with 2 discal glandular ducts; meta-intercoxal process about as long as wide; metasubcoxal line absent. Ventrites with lateral glandular ducts, present on 1-5. Abdominal spiracles present on segments 1-7. Prescutum with variolate microsculpture. Scutellum transverse. Epipleuron present to level of posterior margin of metasternum. Hind wing reduced; marginal setae present to level of RA+ScP vein; basal binding patch present; veins MP_3, MP_4+CuA_1, and CuA_{3+4} absent. Tarsal formula 555; tarsomeres distinctly lobed, tarsomere 3 of pro- and metatarsi and 2 and 3 of mesotarsus dilated.

Female.— Spermatheca bulb-like; spermathecal duct sclerotized, coiled.

Male.— Orientation of aedeagus unknown. Spiculum gastrale asymmetrical, broad.

Diet.— Fungal spores and hyphae (personal observation).

Habitat.— Leaf litter (unpublished data).

Distribution.— New Zealand.

Discussion.— The genus *Salltius* is monotypic. Among south temperate atomariines, *Salltius* is unique in having the cephalic glandular ducts joined at the middle and a body form which is similar to that found among members of the family Scydmaenidae.

Genus *Tisactia* Casey
(Figs. 207)

Tisactia Casey, 1900:108. Type species: *Tisactia subglabra* Casey, 1900, by monotypy.

Diagnosis.— Body form convex; pronotal sides slightly converging anteriorly, greatest width near middle. Antennal club 3-segmented. Cephalic glandular ducts not fused in middle. Antennal grooves on head and prosternum absent. Pronotum with lateral marginal bead narrow. Prosternum with parallel lines; anterior glands present. Mesosternal glands not opening onto callus. Metasubcoxal lines absent. Tarsal formula 555; tarsomeres slightly lobed.

Description.— Length 1.1-1.3 mm. Color of body light or dark brown. Body form convex, parallel-sided. Body setae sparse, short. Prosternal area without punctation. Head not constricted behind eye; boss on front of head absent; clypeus on same level as that of frons; antennal grooves absent; cephalic glandular ducts not fused at middle. Eye prominent; ocular setae present. Antenna with 3-segmented club; antennomere 11 subequal to that of 10; antennomere 3 up to 3x the length of 4; shape of funicle not conical and curved. Mandible with 1 dorsal tubercle; basal sensory pores present. Mentum with median process; transverse line or ridge absent. Pronotal sides slightly converging anteriorly, greatest width near middle; marginal bead narrow. Hypomeron with notch near procoxal cavity. Prosternal process with parallel lines; anterior region of prosternum with glandular ducts; antennal grooves absent. Procoxal cavity externally open. Mesepimeron without pit. Mesosternum with parallel lines; glandular ducts not opening onto a callus. Width of mesosternal process greater than that of mesocoxa. Metasternum without a median longitudinal line. Ventrite 1 with 2 discal glandular ducts; meta-intercoxal process wider than long; metasubcoxal line absent. Ventrites with lateral glandular ducts, present on 1-5. Abdominal spiracles absent from segments 6 and 7. Prescutum with variolate microsculpture. Scutellum transverse. Epipleuron present at or beyond level of posterior margin of metasternum. Hind wing present; marginal setae present to level of RA+ScP vein; basal binding patch poorly developed or absent; veins MP_3, MP_4+CuA_1, and CuA_{3+4} absent. Tarsal formula 555; tarsomeres slightly lobed.

Female.— Spermathecal duct unsclerotized.

Male.— Spiculum gastrale symmetrical, broad. Tarsomeres 1-3 of pro- and mesotarsi dilated.

Diet.— Fungal spores and hyphae (personal observation).

Habitat.— Rotting vegetation, leaf litter (K. Stephan personal communication; personal observation).

Distribution.— North America.

Discussion.— The genus *Tisactia* contains one described species; however, three undescribed species have been examined. This genus is closely related to members of the genera *Curelius* and *Ephistemus*.

TRIBE CRYPTAFRICINI

Cryptafricini, new tribe. Type genus: *Cryptafricus*, new genus.

Diagnosis— Body form short, oval in most species. Conspicuous glandular ducts present in body (absent in *Cryptafricus*). Frons with tubercle. Posterior portion of tentorium narrow and straplike. Pronotal bead present (distinct in posterior half in some species). Prosternum short in front of coxa. Tibia without apical spines.

Description.— Body form short, oval in most species. Conspicuous glandular ducts present in body (absent in *Cryptafricus*); pores associated with setae in most species. Head with eye well developed; frons with tubercle; mandible with well developed sensory pores; width of palpomere 1 greater than that of palpomere 2; gular sutures present; posterior portion of tentorium narrow and straplike. Pronotum with lateral margin unmodified or with

angularity (*Microphagus, Cryptogasterus*, and some *Anitamaria*); marginal bead present. Hypomeron without notch above procoxal cavity (present in *Cryptafricus*). Procoxal cavity internally closed; externally closed. Prosternum short in front of coxa; anterior glandular ducts absent. Mesosternal glandular ducts absent. Metasternum without longitudinal line (present in some *Microphagus* and *Anitamaria*). Ventrite 5 sinuate or evenly arcuate; asperities present. Hind wing present; veins MP_3, MP_4+CuA_1, CuA_{3+4}, CuA_{3+4}+AA_{1+2} absent; basal binding patch absent. Tibia without apical spines; 1 apical spur present.

Male.— Aedeagus with arms of tegmen broadly connected; endophallus notched apically (aedeagus of *Cryptafricus* reduced). Spiculum gastrale narrow or broad (*Cryptafricus*).

Female.— Ovipositor poorly developed. Spiculum gastrale absent. Spermathecal duct unsclerotized.

Discussion.— The tribe Cryptafricini contains four genera that are described below.

Cryptafricus Leschen, new genus
(Figs. 22, 38, 57, 72, 83, 88, 103, 108, 123, 201)

Type species: *Cryptafricus leleupi* Leschen, new species

Diagnosis.— Body form elongate; more or less parallel-sided. Antennal club 2-segmented. Glandular ducts in body absent. Pronotum compressed at sides; marginal bead present throughout. Pronotal angularity absent. Tarsal formula 444.

Description.— Length 1.7-1.8 mm. Body color dark brown. Body form elongate, more or less parallel-sided. Body setae long, decumbent. Prosternal area without punctation; microsculpture alveolate. Glandular ducts of body absent. Head without line on vertex; frons without tubercle; gular sutures absent. Eye prominent; ocular setae absent. Antenna with 2-segmented club; length of antennomere 11 2x that of antennomere 10. Pronotum compressed at sides; lateral marginal bead present throughout; angularity absent. Hypomeron with a notch near the procoxal cavity. Mesosternum without parallel lines; procoxal rests absent. Mesosternal process without internal lateral processes; width of mesosternal process less than 1/3 that of mesocoxa. Metasternum without a median longitudinal line; submesocoxal bead narrow. Metendosternite with basal plate transverse. Meta-intercoxal process wider than long; metasubcoxal line absent. Posterior margin of ventrite 5 evenly arcuate. Abdominal spiracles absent from segments 6 and 7. Prescutum with variolate microsculpture; anterior setae absent. Epipleuron present to level of posterior margin of metasternum. Hind wing with marginal setae present to level of RA+ScP vein. Tibia with 2 apical spurs. Tarsal formula 444.

Female.— Not examined.

Male.— Aedeagus reduced to 2 sclerites. Spiculum gastrale, symmetrical, broad. Metasternum without setiferous patch.

Diet.— Fungal spores and hyphae (personal observation).

Habitat.— Leaf litter.

Distribution.— Eastern Zaire.

Discussion.— The genus *Cryptafricus* is proposed for a species that has an unusual combination of characters. *Cryptafricus* is sister taxon to the remaining species of Cryptafricini.

Etymology.— The generic name is derived from the Greek word kryptos, referring to the family name Cryptophagidae and the name of the continent Africa.

Cryptafricus leleupi Leschen, new species
(Figs. 22, 38, 57, 72, 83, 88, 103, 108, 123, 201)

Description.— Length 1.70-1.80 mm (n = 4). Color of body light or dark brown; elytron lighter around margin in some specimens; mouthparts, legs, antennomeres 1-7 light brown. Punctation moderately dense, average width of puncture 0.001 mm; microsculpture alveolate throughout body. Body setae long, decumbent; average length 0.005 mm. Head sparsely punctate, punctures separated by about 1 diameter; interantennal distance = 0.018 mm. Eye prominent; finely faceted. Antenna elongate, extending to basal 1/3 of pronotum; antennomere relative lengths 11:8:6:4:5:3:3:3:3:5:10. Pronotum sinuate; about 0.94 x as long as wide (PL/MPW = 0.85 - 1.03 , x = 0.94); depth = 0.30 - 0.40, x = 0.35 mm; punctures of disk poorly defined, meshing with microsculpture, separated by about 1.5 diameter. Prosternal process narrow, width 1/5 that of procoxa; longer than anterior portion of prosternum. Elytra about 1.48 x as long as wide (EL/MEW = 1.42 - 1.50, x = 1.62) and 3.10 x as long as pronotum (EL/PL = 2.92 - 3.38, x = 3.10); punctures separated by 1.5 diameters. Submesocoxal bead narrow. Metasternal process quadrate. Aedeagus as in Fig. 108.

Discussion.— This is the only member of the genus *Cryptafricus*, and it can be recognized easily by those characters mentioned in the diagnosis for the genus.

Etymology.— Named in honor of N. Leleup, collector of the type series and for his fondness of small beetles, particularly Pselaphidae.

Type.— Holotype, with labels as follows, "I.R.C.S.A. - Mus. Congo. Kivu: Lac Lungwe, 2600 m, V-1958. B. 16. N. Leleup. Biot. No. 16. sols suspendus, HOLOTYPE *Cryptafricus leleupi* R. Leschen 1994" (MRAC).

Paratypes.— ZAIRE: 2, Same data as holotype (1 on microslide) (MRAC, RALC); 2, same data as holotype except terr. Uvira (MRAC).

Cryptogasterus Leschen, new genus
(Figs. 20, 58, 68, 68a, 96, 102, 109, 110, 161, 203)

Type species: *Cryptogasterus lawrencei* Leschen, new species

Diagnosis.— Body oval; more or less parallel-sided. Antennal club 3-segmented. Glandular ducts present in body. Pronotum not compressed at sides; bead present in basal half. Pronotal narrow process present. Tarsal formula 555.

Description.— Length 1.4-1.7 mm. Color of body tan, light or dark brown. Body form short, oval; more or less parallel-sided. Body setae moderately elongate, decumbent. Prosternal area without punctation. Head with line on vertex; frons with tubercle; gular sutures present; cephalic glands present. Eye prominent; ocular setae present. Antenna with 3-segmented club; antennomere 11 subequal to that of antennomere 10. Pronotum marginal bead narrow, distinct in basal half; narrow process or angularity present. Hypomeron without a notch near the procoxal cavity. Mesosternum with parallel lines; procoxal rests absent. Mesosternal process with internal lateral processes; width of mesosternal process 2/3 that of mesocoxa. Metasternum without discal glandular duct; submesocoxal bead wide; median longitudinal line absent. Metendosternite with basal plate wide at base. Meta-intercoxal process wider than long; metasubcoxal line absent. Ventrites with lateral glandular ducts associated with setae, present on 2-4. Posterior margin of ventrite 5 sinuate. Abdominal spiracles absent from segments 5 to 7. Prescutum without microsculpture; anterior setae present. Epipleuron present beyond level of edge of metasternum. Hind wing with marginal setae present beyond level of RA+ScP vein. Tibia with 1 apical spur. Tarsal formula 555.

Male.— Aedeagus well developed; orientation vertical in body. Spiculum gastrale asymmetrical, narrow. Metasternum without setiferous patch.

Diet.— Fungal spores (personal observation).

Habitat.— Gasteromycetes.

Larval descriptions.— Larvae not described.

Distribution.— Eastern Australia.

Discussion.— The genus *Cryptogasterus* is monotypic and is described for a species that is commonly encountered in puffballs (Gasteromycetes). *Cryptogasterus* is sister taxon to *Anitamaria*.

Etymology.— The generic name is a combination of the Greek words kryptos, referring to the family name Cryptophagidae, and gaster, referring to the occurrence of the type species on Gasteromycetes.

***Cryptogasterus lawrencei* Leschen, new species**
(Figs. 20, 58, 68, 68a, 96, 102, 109, 110, 161, 203)

Description.— Length 1.40-1.66 mm (n = 10). Color of body tan, light or dark brown; elytron infuscate in some specimens; front of head, mouthparts, legs, antennomeres 1 - 8 light brown. Punctation moderately dense, average width of puncture 0.001 mm. Body setae decumbent; average length 0.005 mm. Head sparsely punctate, punctures separated by about 3-4 diameters; interantennal distance = 0.014 mm. Eye prominent; finely faceted. Antenna elongate, extending to basal 1/3 of pronotum; antennomere relative lengths 8:8:5:3:4:3:3:3:4:4:5. Pronotum slightly constricted anteriorly; about 0.69 x as long as wide (PL/MPW = 0.61 - 0.76 , x = 0.69); depth = 0.39 - 0.47, x = 0.44 mm; punctures of disk sparse, separated by about 2 diameters. Prosternal process equal in length to anterior portion of prosternum; not extending beyond procoxa; subdepressed posteriorly. Elytra about 1.31 x as long as wide (EL/MEW = 1..11 - 1.46, x = 1.31) and 2.77 x as long as pronotum (EL/PL = 2.55 - 3.01, x = 2.77); punctures separated by 2 diameters. Submesocoxal bead wide. Metasternal process slightly quadrate. Aedeagus as in Figs. 109, 110.

Discussion.— Specimens of this species vary in color from dark to light brown. Many specimens encountered are teneral which suggests that adults may remain in puffball colonies for more than one generation.

Etymology.— Named in honor of J. F. Lawrence, an authority on beetle systematics and biology and one of the collectors of the type series.

Type.—Holotype, with labels as follows, "Mt. Glorious, 630 m QLD, 14 Nov. 1986, collected T. Hiller, flight intercept trough trap, rainforest, HOLOTYPE *Cryptogasterus lawrencei* R. Leschen 1994" (ANIC).

Paratypes.— 93. AUSTRALIA: NEW SOUTH WALES. 1, Berlington House, 40 km NW Dungog, 400m, 11 June - 28 Aug. 1982, S. & J. Peck, FIT, Sclerophyll forest (ANIC); 1, Ben Boyd N.P., Bittangabee nr. Green Cape, 16-19 Feb. 1984, J. Lawrence, Flight intercept/ window trough trap (ANIC); 1, Lorien Wildlife Refuge, Lansdowne via Taree, Dec. 1986, H & A Howden, flight intercept trap (ANIC); 3, Wiangaree SF, 600 m, Sheepstation Ck, 29.II - 3.III.1980, subtrop.rainfor, A. Newton, M.Thayer, In Puffballs (ANIC); 4, same except 13 June - 24 August, S & J Peck (ANIC); 4, Mt. Keira Scout Camp, Woollongon, 4-5 Mar. 198, 81-2, puffballs, J. F. Lawrence, Coll (ANIC); 2, same except at 320m on *Lycoperdon perlatum*, Lot 81-2 (ANIC); 5, Wiangaree S. F. Brindle Ck. 740 m, 3.III.1980, A. Newton, M. Thayer, In puffballs (ANIC); 1, same except Berlesed from log and leaf litter (ANIC); 1, 28.48S 152.59E, Richmond Range S.F., c600m 13-14 Feb. 1983, T. Weir and A. Calder, Berlesate, ANIC 774, Closed forest (ANIC); QUEENSLAND. 7, same as Holotype (ANIC); 4, Mt. Lewis, 20 km SW Mossman, 1000m, 26 June - 1 Aug. 1982. S & J Peck, FIT rainforest (ANIC); 40, Joalah NP. 18-20.X.1978, 78-153, John F. Lawrence, Coll (ANIC, RALC, FMNH, MANC, SEMC, USNM, MNHG, PARI); 7, same except Tamborine Mt., 18-21 Oct 1978 (lot #78-153) (ANIC); 2, (1 on microslide) same except 27.56S 153.12E, *Lycoperdon* sp. (ANIC, RALC); 1, 28.14S 153.08E Lamington N.P. (O'Reillys), 2-4 Mar 1980, J.F. Lawrence, lot 80-32, Unidentified puffballs (ANIC).

***Anitamaria* Leschen, new genus**
(Figs. 13, 23, 61, 71, 80, 86, 101, 104, 129, 136, 141, 151, 153, 155, 158, 165, 168, 169, 200)

Type species: *Anitamaria thayerorum* Leschen, new species

Diagnosis.— Body form elongate oval; more or less parallel-sided. Antennal club 3-segmented. Glandular ducts in body present. Pronotum not compressed at sides; bead present in basal half. Pronotal angularity present or absent. Tarsal formula 555.

Description.— Length 1.0-2.1 mm. Color of body light or dark brown. Body form elongate or elongate oval; more or less parallel-sided. Body setae moderately long, suberect or decumbent. Prosternal area with or without punctation. Head with line on vertex; clypeus on same plane as that of frons; frons with tubercle; gular sutures present; cephalic glands present. Eyes prominent; ocular setae present or absent. Antenna with 3-segmented club; length of terminal antennomere 2x to that of antennomere 10; third antennomere up to 2x the length of fourth; shape of funicle not conical and curved. Mandible without dorsal tubercles; basal sensory pores present. Pronotum marginal bead narrow, distinct in basal half; narrow process or angularity present. Hypomeron without a notch near the procoxal cavity. Mesosternum with parallel lines; procoxal rests present or absent. Mesosternal process with internal lateral processes; width 2/3 of that of mesocoxa. Metasternum with discal glandular duct, associated setae present; submesocoxal bead narrow or wide; longitudinal line present or absent. Metendosternite with basal plate trapezoidal. Meta-intercoxal process wider than long; metasubcoxal line absent. Ventrites with lateral glandular ducts, present on 2-4. Posterior margin of ventrite 5 sinuate. Abdominal spiracles absent from segments 5 - 7. Microsculpture of prescutum variolate or absent; anterior setae present. Epipleuron distinct to or beyond level of edge of metasternum. Hind wing with marginal setae present to level beyond RA+ScP vein;. Tibia with 1 apical spur. Tarsal formula 555.

Male.— Aedeagus well developed; orientation in body vertical or horizontal. Spiculum gastrale symmetrical or asymmetrical, narrow in width. Metasternum without setiferous patch.

Diet.— Fungal spores (personal observation).

Habitat.— Leaf litter, rotting logs.

Distribution.— Circumtropical, Australia, South Africa.

Discussion.— The genus *Anitamaria* is described for several species in the tribe Cryptafricini. This genus is widely distributed and contains at least nine species which were collected from flight intercept traps and sifting leaf litter. Additional specimens produced by mass collecting techniques in remote tropical areas will probably yield more species. A revision and cladistic analysis of the members of *Anitamaria* would be interesting for addressing questions about biogeography. *Anitamaria* is sister taxon to *Cryptogasterus*.

Etymology.— The generic name is derived from the root word *Atomaria*, a genus that the type species closely resembles, and the Greek woman Anita Davelos.

***Anitamaria thayerorum* Leschen, new species**
(Figs. 23, 61, 71, 101, 104, 200)

Description.— Length 1.33-1.57 mm (n = 10). Color of body light or dark brown. Punctation sparse; present in prosternal area; average width of puncture 0.001 mm. Body setae moderately elongate, biseriate, decumbent; average length 0.004 mm. Head with punctures separated by about 1 diameter; interantennal distance = 0.012 mm. Eye prominent; finely faceted; ocular setae absent. Antenna elongate, extending beyond base of pronotum; antennomere relative lengths 5:5:3:3:4:3:4:3:5:5:8. Pronotum constricted anteriorly; about 0.68 x as long as wide (PL/MPW = 0.63 - 0.73 , x = 0.68); depth = 0.38 - 0.42, x = 0.40 mm; punctures of disk separated by about 1 diameter; base of disk without areolate microsculpture. Prosternal process equal in length to anterior portion of prosternum; extending posteriorly beyond procoxa. Elytra about 1.31 x as long as wide (EL/MEW = 1.21 - 1.39, x = 1.31) and 3.12 x as long as pronotum (EL/PL = 2.84 - 3.37, x = 3.12); punctures separated by 1.5 diameters. Mesosternum without procoxal rests. Metasternum without longitudinal line; submesocoxal bead narrow, without small punctures. Metasternal process quadrate. Prescutum with variolate microsculpture; anterior setae equal in length to that of scutellum. Epipleuron to level of posterior edge of metasternum. Aedeagus as in Fig. 104. Spiculum gastrale of male asymmetrical.

Diet.— Fungal spores (personal observation).

Habitat.— Bark of *Nothophagus moorei*.

Distribution.— Eastern Australia.

Discussion.— This species can be distinguished from other members of *Anitamaria* by its smaller size, elongate antennae which extends beyond the base of the pronotum, basal disk of pronotum without areolate microsculpture, and submesocoxal bead narrow that does not have small punctures.

Etymology.— Named in honor of Alfred Newton and Margaret Thayer, dedicated collectors, beetle enthusiasts, and staphyliniform researchers.

Type.—Holotype, with the following labels, "Australia: NSW: Wiangaree SF, Brindle Ck, 740 m, 29.II - 3.III. 1980, Subtrop. Rainfor., A. Newton, M. Thayer Pyrethrin fogging *Nothofagus moorei* bark, HOLOTYPE *Anitamaria thayerorum* R. Leschen 1994" (ANIC).

Paratypes.—7. AUSTRALIA: NEW SOUTH WALES. 3, same as Holotype (ANIC, MANC); 2, 28.22S 153.05E, Brindle Ck., Border Ra. NP, 3-14 Oct. 1984, I. Naumann, J. Cardale, ex. pantraps (ANIC). QUEENSLAND. 1 (on microslide), Kirrama St. For., 32 km NW Cardwell, 800m, 23 June- 8 Aug. 1982, S & J Peck SBP46, FIT, rainforest (RALC); 1 (on microslide), 40 km W Ingham, nr. Wallaman Falls, 22 Jun. - 7 Aug. 1982, S & J. Peck, coll. SBP 45, 600 m. FIT, rainforest (RALC).

Microphagus Leschen, new genus
(Figs. 35, 62, 67, 81, 87, 99, 106, 107, 206)

Type species: *Microphagus johnsoni* Leschen, new species

Diagnosis.— Body form slightly elongate oval; more or less parallel-sided. Antenna incrassate. Glandular ducts in body present. Pronotum not compressed at sides; lateral marginal bead present in basal half. Pronotal angularity present. Tarsal formula 555.

Description.— Length 0.80-1.1 mm. Color of body light, dark, or chocolate brown. Body form slightly elongate; more or less parallel-sided. Body setae short, decumbent. Prosternal area without punctation. Head without line on vertex; frons with tubercle; gular sutures present; cephalic ducts present. Eye more or less prominent; ocular setae absent. Antenna incrassate; length of antennomere 11 2x that of antennomere 10. Pronotum marginal bead narrow, present throughout; angularity present. Lateral margin of pronotum with 1 glandular duct. Hypomeron without a notch near the procoxal cavity. Mesosternum with parallel lines; procoxal rests present. Mesosternal process without internal lateral processes; width of mesosternal process less than 1/3 that of mesocoxa. Metasternum with longitudinal line present or absent; submesocoxal bead wide; discal glandular duct present, without associated setae. Metendosternite with basal plate trapezoidal. Meta-intercoxal process about as long as wide; metasubcoxal line absent. Ventrites with lateral glandular ducts, present on 1-5. Posterior margin of ventrite 5 sinuate. Abdominal spiracles present on segments 1-7. Prescutum with variolate microsculpture; anterior setae absent. Epipleuron distinct beyond level of posterior edge of metasternum. Hind wing with marginal setae present to level of RA+ScP vein; basal binding patch absent. Tibia with 1 apical spur. Tarsal formula 555.

Male.— Aedeagus well developed; orientation vertical in body. Spiculum gastrale asymmetrical, narrow in width. Metasternum with a setiferous patch.

Diet.— Fungal spores and hyphae (personal observation).

Habitat.— Leaf litter.

Distribution.— Central and South America.

Discussion.— The genus *Microphagus* is described for neotropical species representing an undescribed genus of afrocryptine. *Microphagus* is one of the smallest members of Cryptophagidae and is monophyletic based on a variety of unique characters in Atomariinae (e.g., male with setiferous patch on metasternum, a large and conspicuous angularity present on the pronotum, and a narrow mesosternal process). *Microphagus* is sister taxon to *Cryptogasterus* + *Anitamaria*.

Etymology.— The generic name is a combination of the Greek words mikros, meaning small, and phagein, meaning to eat and referring to the family name Cryptophagidae.

Microphagus johnsoni Leschen, new species
(Figs. 35, 62, 67, 81, 99, 106, 107, 206)

Description.— Length 0.83-0.89 mm (n = 2). Color of body chocolate brown; mouthparts, legs, flagellum light brown. Punctation moderately dense, average width of puncture 0.001 mm. Body setae long, decumbent; average length 0.003 mm. Head with punctures separated by about 1.5 diameters; interantennal distance = 0.009 mm. Eye prominent; coarsely faceted. Antenna elongate, extending beyond base of pronotum; antennomere relative lengths 4:5:4:3:4:4:5:3:5:5:6. Pronotum slightly widened anteriorly; about 0.75 x as long as wide (PL/MPW = 0.75 , x = 0.76); depth = 0.17 - 0.19, x = 0.18 mm; punctures separated by about 1 - 2 diameters; base of disk with areolate microsculpture. Prosternal process longer than anterior portion of prosternum; extending beyond procoxa. Elytra about 1.30 x as long as wide (EL/MEW = 1.29 - 1.31, x = 1.30) and 2.58 x as long as pronotum (EL/PL = 2.50 - 2.65, x = 2.58); punctures separated by 1/2 - 1 diameter; areolate microsculpture present. Submesocoxal bead wide. Metasternal evenly arcuate. Aedeagus as in Figs. 106, 107.

Diet.— Fungal spores (personal observation).

Habitat.— Leaf litter.

Distribution.— Ecuador.

Discussion.— *Microphagus johnsoni* can be distinguished from the remaining species that are undescribed by the presence of areolate microsculpture on the pronotum and color of the body.

Etymology.— Named in honor of C. Johnson, another cryptophagid worker and a specialist on small beetles.

Type.—Holotype, male, with labels as follows, "Ecuador: Pichincha Prov. 47 Km S. of Santo Domingo, Rio Palenque Sta. 700', Leg. S. Peck, V:18-30:1975, FM(HD)#75-293, Forest litter (Ber.), HOLOTYPE *Microphagus johnsoni* R. Leschen 1994" (FMNH).

Paratypes.— 2, same as Holotype, 1 on slide (FMNH, RALC).

ACKNOWLEDGMENTS

Above all I thank J. S. Ashe for his perceptive guidance and support through my graduate career. Additional guidance and intellectual support from my committee members, B. Alexander, D. Alexander, W. Bell, R. Lichtwardt, and C. D. Michener and fellow graduate students at the Snow Entomological Museum and Natural History Museum are greatly appreciated. Special thanks go to R. A. Crowson, C. Johnson, and J. F. Lawrence who have been supportive of my research from the very beginning, and they, along with A. Allen, Y. Bousquet, C. E. Carlton, J. Pakaluk, A. Ślipiński, M. Thayer, and M. Thomas, provided specimens of cucujoids for dissection and literature pertinent to this study. C. Johnson and R. A. Crowson and their respective families have been especially kind during my visits studying cryptophagids. I also thank those individuals and museums mentioned previously who contributed cryptophagid specimens for this study and the staff of the Libraries of the University of Kansas and Field Museum of Natural History. For commentary on cryptophagid biology and systematics I thank R. A. Crowson, C. Johnson, J. F. Lawrence, C. Marshall, K. Richards, D. Roubik, F. Silveira, P. Skelley, and K. Stephan. B. Horn and R. Lichtwardt identified some of the fungal hosts that cryptophagids utilize. A. Davelos provided emotional support, while S. Lingafelter helped with miscellaneous chores. SEM and other technical assistance was provided by B. Cutler. The manuscript benefited from final review by C. Johnson. Lastly, I thank J. Weaver for administrative and technical assistance which facilitated much of my work.

This research was supported by a National Science Foundation doctoral dissertation improvement grant (DEB-9222863) to J.S. Ashe and R. Leschen and a University of Kansas Graduate Student Fellowship.

LITERATURE CITED

Arnett, R. H. 1968. The Beetles of the United States. (A Manual for Identification). American Entomol. Inst., Ann Arbor, xii + 1112 pp.

Audisio, P. 1994. Nitidulidae - Kateretidae. Fauna d'Italia, vol. 32. Edizioni Calderini, Bologna, 997 pp.

Austin, E.P. 1880. Supplement to the check list of the Coleoptera of America, north of Mexico. Boston, 67 pp.

Baudi, F. 1870. Coleopterorum messis in insula Cypro et Asia minore ab Eugenio Truqui congregatae recensitio; de Europeis notis quibusdam additis (pars tertia). Berl. Entomol. Zeitschr., 14: 49-90.

Benick, L. 1952. Pilzkäfer und Käferpilze. Ökologische und statistiche Untersuchungen. Acta Zool. Fennica, 17: 1-250

Blackburn, T. 1891. Further notes on Australian Coleoptera, with descriptions of new species. Trans. Roy. Soc. S. Australia, 14: 65-153.

Blake, D. H. 1928. Two new clavicorns from the United States. Psyche, 35: 108-113.

Blackwelder, R.E. 1945. Checklist of the the Coleopterous Insects of Mexico, Central America, the West Indies, and South America. Part 3. U.S. Nat. Mus. Bull., 185: 343-550.

Blackwell, M. 1984. Myxomycetes and their arthropod associates. pp. 65-90 *in* Q.D.Wheeler, M. Blackwell, eds., Fungus-Insect Relationships. Columbia Univ. Press, New York.

Blisson, J. F. I. 1847. Description de la larve et de la nymphe du *Cryptophagus hirtus* Gyllenhal. Ann. Soc. Entomol. France, 7: 315-325, + pl. 9.

Bollow, H. 1941. Über *Coniophthalma germanicus* Rtt. und die palaearktischen Arten der Gattung *Henoticus* Thoms. (Col. Cryptophagidae). Mitt. Münch. Entomol. Gesell., 31: 569-579.

Bousquet, Y. 1989. A review of the North American genera of Cryptophaginae (Coleoptera: Cryptophagidae). Coleopterists Bull., 43: 1-17.

Böving, A. G. and F. C. Craighead. 1931. An illustrated synopsis of the principal larval forms of the Order Coleoptera. Entomol. Americana (New Series) 11: 1-351.

Brèthes, J. 1922. Descripción de varios Coleópteros de Buenos Aires. Anal. Soc. Cient. Argentina, 94: 263-305.

Broun, T. 1893. Manual of the New Zealand Coleoptera, Parts V, VI, VII. Colonial Museum and Geological Survey Department, Wellington, pp. xvii + 975-1504.

Broun, T. 1910. Descriptions of New genera and species of Coleoptera. Bull. New Zealand Inst. Wellington, 1910: 1-78.

Bruce, N. 1936. Monographie der europäischen Arten der Gattung *Cryptophagus* Herbst. Acta Zool. Fennica, 20: 1-167, + 17 tbls., + 8 maps.

Bruce, N. 1940. Coleoptera-Cryptophagidae von Juan Fernandez *In* C. Skottsberg, The Natural History of Juan Fernandez and Eastern Islands. Vol. III. Zoology. Almqvist and Wiskell, Uppsala, pp. 681-688.

Bruce, N. 1952. Coleoptera-Cryptophagidae in the British Museum, I. Ann. Mag. Nat. Hist. (12) 5: 167-188.

Bruce, N. 1963. Coleoptera Cryptophagidae in Musée Royal de l'Afrique Centrale (V). Rev. Zool. Bot. Afr., 68(3-4): 203-221.

Burakowski, B. and S. A. Slipinski. 1987. A new species of *Protosphindus* (Coleoptera: Sphindidae) from Chile with notes and descriptions of immature stages of related forms. Ann. Mus. Civ. Storia Nat. Genova, 86: 605-625.

Camin, J. H. and R.R. Sokal. 1965. A method for deducing branching sequences in phylogeny. Evolution, 19: 311-326.

Carpenter, J. M. 1988. Choosing among multiple equally parsimonious cladograms. Cladistics, 4: 291-296.

Casey, T. L. 1900. Review of the American Corylophidae, Cryptophagidae, Tritomidae and Dermestidae, with other studies. Jour. New York Entomol. Soc., 8: 51-172.

Casey, T.L. 1924. Additions to the known Coleoptera of North America, Vol. 11. Mem. Coleoptera. New Era, Lancaster, Pennsylvania, 347 pp.

Chaudoir, M. 1845. Notices entomologiques sur le gouvernement et la ville de Kiew. Bull. Soc. Imp. Natural. Moscou, 18: 158-213.

Chavarria, G. 1994a. Phoresy on a neotropical bumblebee (Hymenoptera: Apidae) by *Antherophagus* (Coleoptera: Cryptophagidae). Psyche, 101: 109-111.

Chavarria, G. 1994b. First neotropical mutualistic associations in bumblebee nests (Hymenoptera: Apidae). Psyche, 101: 112-118.

Coombs, C. W. and G. E. Woodroffe. 1955. A revision of the British species of *Cryptophagus* (Herbst) (Coleoptera: Cryptophagidae). Trans. Roy. Entomol. Soc. London, 106: 237-282.

Coombs, C. W., and G. E. Woodroffe. 1962. The taxonomic validity of the genus *Mnionomus* Wollaston, 1864 (Coleoptera: Cryptophagidae). Proc. Roy. Entomol. Soc. London (B), 31: 61-66.

Cooter, J. 1991. Cryptophagidae. pp. 129-131 *in* J. Cooter et al., eds., A Coleopterist's Handbook, Third ed. The Amateur Entomologists' Society, Feltham.

Crotch, G. R. 1873. Check List of the Coleoptera of America, North of Mexico. Naturalists' Bureau, Salem, Massachusettes, 136 pp.

Crowson, R. A. 1955. The Natural Classification of the Families of Coleoptera. Nathaniel Lloyd and Co., London, 187 pp.

Crowson, R. A. 1960. The phylogeny of Coleoptera. Ann. Rev. Entomol., 5: 111-94.

Crowson, R. A. 1967. The natural classification of the families of Coleoptera. Addenda and corrigenda. Entomol. Monthly Mag., 103: 209-214.

Crowson, R. A. 1973. Further observations on Phloeostichidae and Cavognathidae, with definitions of new genera from Australia and New Zealand. Coleopterists Bull. 27: 54-62.

Crowson, R. A. 1980. On amphipolar distribution patterns in some cool climate groups of Coleoptera. Entomol. Generalis, 6: 281-292.

Crowson, R. A. 1981. The Biology of Coleoptera. Academic Press, London, xii + 802 pp.

Crowson, R. A. 1984. The associations of Coleoptera with Ascomycetes. pp. 256-285 *in* Q.D.Wheeler, M. Blackwell, eds., Fungus-Insect Relationships. Columbia Univ. Press, New York.

Curtis, J. 1833. Characters of some undescribed genera and species, indicated in the "Guide to an Arrangement of British Insects". Entomol. Mag., 1: 186-199.

Dajoz, R. 1959. Les espèces françaises du genre *Cryptophagus*. L'Entomologiste, 15: 93-115.

Dajoz, R. 1988. Les Coléoptères d'un polypore (Champignon, Basidiomycète) des montagnes rocheuses (États-Unis), et description de deux espèces nouvelles (Erotylidae et Cryptophagidae). Nouv. Revue Entomol. (N. S.) 5: 209-215.

DeJean, M. 1821 Catalogue de la Collection de Coléoptères. Crevot, Paris, viii + 136 pp.

Delobel, A. and M. Tran. 1993. Les Coléoptères des denrées alimentaires entreposées dans les régions chaudes. Faune tropicale. Vol. 32. Institut Français de Recherche pour le Développement en Coopération Centre Technique de Coopération Agricole et Rurale, 424 pp.

Donisthorpe, H. 1920. The phoresy of *Antherophagus*. Entomol. Rec., 32: 181-187.

Donisthorpe, H. 1935. The British fungicolous Coleoptera. Entomol. Monthly Mag., 71: 21-31.

Eichelbaum, F. 1907. Die Larven von *Cis festivus* Panz. und von *Emphylus glaber* Gyll. Zeitschr. wissen. Insekten-Biol., 3: 25-30.

Emetz, V. M. 1977. Review of the Cryptophaginae (Coleoptera, Cryptophagidae) of the Mongolian People's Republic. Nasekomye Mongolii, 5: 290-298.

Erichson, W. F. 1846. Nomina systematica generum Coleopterorum *in* Agassiz, J. L. R. Nomenclator Zoologicus.... Soloduri, ix + 1135 + 170 pp.

Erichson, W. F. 1848. Naturgeschichte der Insecten Deutschlands. Erste Abtheilung. Coleoptera. Dritter Band. Nicolaischen Buchhandlung, Berlin, 968 pp.

Evans, M. E. G. 1961a. The life history of *Atomaria ruficornis* (Marsh.) (Col., Cryptophagidae). Trans. Soc. British Entomol., 14: 207-222.

Evans, M. E. G. 1961b. The muscular and reproductive systems of *Atomaria ruficornis* (Marsham) (Coleoptera, Cryptophagidae). Trans. Roy. Soc. Edin., 64: 297-399.

Evans, M. E. G. 1961c. The alimentary canal of *Atomaria ruficornis* (Marsham) (Col., Cryptophagidae). Entomologist, 94: 263-273.

Evans, M. E. G. 1964. The tracheal system of *Atomaria ruficornis* (Marsh.) (Col., Cryptophagidae). Entomologist, 97: 250-257.

Falcoz, L. 1921. Description d'un genre nouveau et de deux espèces nouvelles de Cryptophagidae [Col.] du nord de l'Afrique. Bull. Soc. Entomol. France, 23: 42-44.

Falcoz, L. 1922. Etudes sur les Cryptophaginae (Coléoptères Erotylides). II. *Henoticus californicus* Mannerheim, espèce americaine en voie d'acclimatation européenne. Ann. Soc. Linn. Lyon, 69: 167-183.

Falcoz, L. 1924. Etudes sur les Cryptophaginae (Coléoptères Erotylides). IV. Essai sur les larves de *Cryptophagus*. Ann. Soc. Linn. Lyon, 71: 120-127.

Falcoz, L. 1929. Tableaux analytiques des coléoptères de la faune Franco-Rhénane (France, Hollande, Belgique, Région rhénane, Valais): Famille 33: Cryptophagidae. Miscellanea Entomol., 31-32: 1-197.

Farris, J.S. 1969. A successive approximations approach to character weighting. Syst. Zool., 18: 374-385.

Farris, J. S. 1970. Methods for computing Wagner Trees. Syst. Zool., 19: 83-92.

Farris, J.S. 1977. Phylogenetic analysis under Dollo's Law. Syst. Zool., 26: 77-88.

Ganglbauer, L. 1899. Die Käfer Mitteleuropa; die Käfer der österreichisch-ungarischen Monarchie, Deutschlands, der Schweiz, sowie des französchen und italienischen Alpengebietes. Carl Gerold's Sohn, Wien, iii + 1046 pp.

Gozis, M. 1886. Recherche de l'Espèce Typique de Quelques Anciens Genres: Rectifications Synonymiques, et Notes Diverses. Imprimerie Herbin, Montlucon, 36 pp.

Grouvelle, A. 1916. Mémoires Entomologiques. Études sur les Coléoptères. Premier fascicule. Paris, 79 pp.

Harris, R. A. 1979. A glossary of surface sculpturing. Occ. Pap. Bur. California Dept. Agri., 28: 1-31.

Hatch, M. H. 1962. The Beetles of the Pacific Northwest. Part III: Pselaphidae and Diversicornia I. Univ. Washington Press, Seattle, ix + 503 pp.

Heer, 0. 1841. Coleopterorum Helvetica. Pars I, Fasc. 3. Orelli, Fussilini et Sociorum, Turici, xii + 652 pp.

Herbst, J. F. W. 1792. Natursystem aller bekannten in- und auslandischen Insekten, als eine Fortsetzung der von Büffonschen Naturgeschichte. Der Käfer, vol. 4. Ben Joachim Pauli, Berlin, viii + 197 pp.

Hetschko, A. 1930. Cucujidae, Thorictidae (Suppl.), Cossyphodidae (Suppl.). Pars 109: pp. 1-122 *in* W. Junk, Coleopterorum Catalogus. W. Junk, Berlin,

Hicks, E. A. 1959. Check-list on the Occurence of Insects in Birds' Nests. Iowa State College Press, Ames, 681 pp.

Hicks, E. A. 1962. Check-list on the occurence of insects in birds' nests. Supplement I. Iowa State Jour. Sci., 36: 233-348.

Hicks, E. A. 1971. Check-list on the occurence of insects in birds' nests. Supplement II. Iowa State Jour. Sci., 46: 123-338.

Hingley, M. R. 1971. The ascomycete fungus, *Daldinia concentrica*, as a habitat for animals. Jour. Animal Ecol., 40: 17-32.

Hinton, H. E. 1945. A Monograph of the Beetles Associated with Stored Products. Volume I. British Museum (Natural History), London, 443 pp.

Hinton, H. E. and F. L. Stephens. 1941. Notes on the biology and immature stages of *Cryptophagus acutangulus* Gyll. (Col., Cryptophagidae). Bull. Entomol. Res., 32: 135-143.

Hisamatsu, S. 1962. A new species of *Cryptophagus* (Col.: Cryptophagidae). Niponius. Acta Coleopt., 1(20): 1-3.

Holdhaus, K. 1903. Beitrage zur Kenntnis der Koleopterengattung *Atomaria* Steph. Münch. Koleopt. Zeitschr., 1: 350-382.

Horion, A. 1960. Faunistik der mitteleuropäischen Käfer. Band VII: Clavicornia. 2. Teil (Sphaeritidae bis Phalacridae). Teredilia, Coccinellidae. A. Feyel, Überlingen, xiii + 375 pp.

Jacquelin du Val, C. 1859. Manuel Entomologique. Genera des Coléoptères d'Europe .... Tome deuxieme. A. Deyrolle, Paris. pp. 90-204, + Catalogue, pp. 111-114, + pls. 48-52.

Johnson, C. 1970. The *Atomaria* species (Col. Cryptophagidae) of Madeira and the Canary Islands including data on the Wollaston collections and lectotype designations for his species. Entomol. Scand., 1: 145-160.

Johnson, C. 1971. The forgotten genus *Curelius* Casey in relation to *Ephistemus* Stephens, with keys to the Palaearctic species (Col., Cryptophagidae). Entomol. Blätter, 66: 159-162.

Johnson, C. 1972. A new North American species of *Henoticoides* Hatch (Col., Cryptophagidae). Entomologist, 105: 274-276.

Johnson, C. 1973. The *Atomaria gibbula* group of species (Coleoptera: Cryptophagidae). Reichenbachia, 14: 125-141.

Johnson, C. 1975a. The Himalayan species of *Henoticus* Thomson (Coleoptera: Cryptophagidae). Senckenbergiana biol., 56(1/3): 37-38.

Johnson, C. 1975b. The *Atomaria* species (Col., Cryptophgidae) of Madeira and the Canary Islands: a supplement. Vieraea, 5: 33-37.

Johnson, C. 1992. Cryptophagidae. pp. 114-136 *in* G.A. Lohse, W.H. Lucht, Die Käfer Mitteleuropas, Supplementband mit Katalogteil, Vol. 13. Goecke and Evers, Krefeld.

Johnson, C. 1993. Provisional atlas of the Cryptophagidae-Atomariinae (Coleoptera) of Britain and Ireland. Biological Records Centre, Huntington, 91 pp.

Johnson, C. and R.A.B. Leschen. In preparation. World catalogue of the species of Cryptophagidae (Coleoptera: Cucujoidea).

Kangas, E. 1963. *Henoticus germanicus* Reitt. als Vertreter einer neuen Cryptophagidengattung, *Coniophthalma* n. gen. (Col.). Ann. Ent. Fenn., 2: 67-73.

Karaman, Z. 1961. Kopulationsapparat des genus *Thelmatophilus* (Cryptophagidae, Col.). Proc. Inter. Cong. Entomol., 11: 71-74.

Kieseritzky, V. and A. Reichardt. 1936. Zur Frage über die Selbständigkeit der Familie Catopochrotidae, im Zusammenhang mit der Entdeckung einer neuen Gattung. Trav. Inst. Zool. Acad. Sci. URSS, 3: 693-697.

Kirby, W. 1837. The Insects *in* J. Richardson, Fauna Boreali-Americana; .... J. Fletcher, Norwich, xxxix + 325 pp. + pls. I-VIII.

Kistner, D. H. 1982. The social insects' bestiary. pp. 361-423 *in* H. R. Hermann, ed., Social Insects, Vol. III. Academic Press, New York.

Klippel, R. 1952. Beiträge zur Kenntnis der Schimmel- und Moderkäfer. Zeitschr. hyg. Zool. Schädl., 40: 65-85.

Kluge, A. G. 1988. A concern for evidence and a phylogenetic hypothesis of relationships among *Epicrates* (Boidae, Serpentes). Syst. Zool., 38: 7-25.

Kluge, A. G. and A. J. Wolfe. 1993. Cladistics: What's in a word. Cladistics, 9: 183-199.

Koch, K. 1989. Die Käfer Mitteleuropas, Ökologie, Band 2. Goecke and Evers, Krefeld, 382 pp.

Kukalová-Peck, J. and J. F. Lawrence. 1993. Evolution of the hind wing in Coleoptera. Canadian Entomol., 125: 181-258.

Lawrence, J. F. 1982. Coleoptera. pp. 482-553 *in* S. P. Parker, ed., Synopsis and Classification of Living Organisms, Vol. 2. McGraw-Hill, New York.

Lawrence, J. F. 1988. Mycophagy in the Coleoptera: Feeding strategies and morphological adaptations. pp. 1-23 *in* N. Wilding, N. M. Collins, P. M. Hammond, J. F. Webber, eds., Insect-Fungus Interactions. Academic Press, London.

Lawrence, J. F. 1991. Chapters on Coleoptera, Sphindidae, Nitidulidae, Rhizophagidae, Boganiidae, Phloeostichidae, Heloti-

dae, Cucujidae, Phalacridae, Hobartiidae, Cavognathidae, Cryptophagidae, Languriidae, Erotylidae. pp. 455-475 *in* F.W. Stehr, Immature Insects, Vol. 2. Kendall-Hunt, Dubuque.

Lawrence, J. F. and E. B. Britton. 1991. Coleoptera. pp. 543-683 *in* The Insects of Australia: a Textbook for Students and Researchers, Vol. II. Second ed., Cornell University Press, Ithaca.

Lawrence, J. F. and A. F. Newton, Jr. 1982. Evolution and classification of beetles. Ann. Rev. Ecol. Syst., 13: 261-290.

LeConte, J. L. 1861. Classification of the Coleoptera of North America, Part I. Smithsonian Miscellaneous Collections, 3: i-xxv + 1-286.

Leng, C. W. 1920. Catalogue of the Coleoptera of America, North of Mexico. The Cosmos Press, Cambridge, x + 470 pp.

Leschen, R. A. B. 1993. Evolutionary patterns of feeding in selected Staphylinoidea (Coleoptera): shifts among food textures. pp. 59-104 *in* C.W. Schaefer, R. A. B. Leschen, eds., Functional Morphology of Insect Feeding. Thomas Say Publications in Entomology: Entomol. Soc. America, Lanham, Maryland.

Leschen, R. A. B. and C. E. Carlton. 1993. Debris cloaking in Endomychidae: a new species from Peru (Coleoptera). Zool. Jour. Linn. Soc., 109: 35-51.

Leschen, R. A. B. and J. F. Lawrence. 1991. Fern sporophagy in Coleoptera from the Juan Fernandez Islands, Chile, with descriptions of two new genera in Cryptophagidae and Mycetophagidae. Syst. Entomol., 16: 329-352.

Lipscomb, D. L. 1992. Parsimony, homology and the analysis of multistate characters. Cladistics, 8: 45-65.

Ljubarsky, G. Y. 1987a. Review of species of the genus *Sternodea* Reitter, 1875 (Coleoptera: Cryptophagidae: Atomariinae). Byulleten' Moskovskogo. Obshchestva Ispytatelei Prirody, Otdel Biologicheskii (N.S.), 92: 53-62

Ljubarsky, G. Y. 1987b. New species of Cryptophagid beetles (Coleoptera: Cryptophagidae) in the fauna of the USSR. Zool. Zhur., 66: 951-954.

Ljubarsky, G. Y. 1989. New taxa of Cryptophagidae beetles in fauna of the USSR. Byulleten' Moskovskogo. Obshchestva Ispytatelei Prirody, Otdel Biologicheskii (N.S.), 94: 49-62.

Ljubarsky, G. Y. 1992a. Functional morphology of bulldozer structures and diversity of vital forms in the family Cryptophagidae (Coleoptera: Clavicornia). Russian Entomol. Jour., 1(1): 3-16.

Ljubarsky, G. Y. 1992b. Beetles of the genus *Cryptophagus* (Coleoptera, Cryptophagidae) from the Caucasus. Zool. Zhur., 71: 68-82.

Ljubarsky, G. Y. 1992c. Cryptophagidae (Coleoptera) of northeast Russia. Zool. Zhur., 71: 83-89.

Ljubarsky, G. Y. 1992d. On the taxonomical status of the genera *Myrmedophila* Bousquet, 1989 and *Catopochrotides* Kies. & Rchdt., 1936 (Coleoptera, Cryptophagidae). Zool. Zhur., 71: 595-598.

Lohse, G. A. 1967. Cryptophagidae. pp. 110-158 *in* H. Freude, K. W. Harde, K. W., G. A. Lohse, Die Käfer Mitteleuropas, Band 7, Clavicornia. Goecke and Evers, Krefeld.

Maddison, D. R. 1991. The discovery and importance of multiple islands of most-parsimonious trees. Syst. Zool., 40: 315-328

Maddison, W. P. 1993. Missing data versus missing characters in phylogenetic analysis. Syst. Zool., 42: 576-581.

Maddison, W. P. and D. R. Maddison. 1992. MacClade, version 3: Analysis of phylogeny and character evolution. Sinauer, Sunderland.

Maddison, W. P., Donoghue, M. J., and D. R. Maddison. 1984. Outgroup analysis and parsimony. Syst. Zool., 33: 83-103.

McHugh, J. 1992. A revisionof *Eurysphindus* LeConte (Coleoptera: Cucjoidea: Sphindidae) and a review of sphindid classification and phylogeny. Syst. Entomol., 18: 57-92.

Meer Mohr, J. C. van der and M. A. Lieftinck. 1947. Over de biologie van *Antherophagus ludekingi* Grouv. (Col.) in hommelnesten (*Bombus* Latr.) op Sumatra. Tijdschrift Entomol., 88(1945): 207-214.

Mickovich, M. F. 1982. Transformation series analysis. Syst. Zool., 31: 461-478.

Mickovich, M. F. and S. J. Weller. 1990. Evolutionary character analysis: tracing character change on a cladogram. Cladistics, 6: 137-170.

Miyamoto, M. M. 1985. Consensus cladograms and general classifications. Cladistics, 1: 186-189.

Mjöberg, E. 1906. Om några svenska insekters biologi och utneckling. Ark. Zool., 3:1-20, + 1 pl.

Motschulsky, V. 1839. Coléoptères du Caucase et des provinces Transcaucasienees décrits par T. Victor. Bull. Soc. Imp. Natural. Moscou, 12: 68-93.

Motschulsky, V. 1844. Bemerkungen zu dem im V^{ten} Bande der Zeitschrift für die Entomologie p. 192 von H.^{rn} Mærkel gegebenen "Beitræge zur Kenntniss der unter Ameisen Lebenden Insekten." Bull. Soc. Imp. Natural. Moscou, 17:812-823.

Nakane, T. and S. Hisamatsu. 1963. Two new genera and three new species of clavicorn Coleoptera from Japan. Fragm. Coleopt., 12: 48-50.

Newport, 1850. Note on *Cryptophagus cellaris*. Trans. Linn. Soc. London, 20: 351-353.

Newton , H. C. F. 1932. On *Atomaria linearis* Stephens (Coleoptera, Cryptophagidae) and its larval stages. Ann. Appl. Biol., 19: 87-97, + 4 figs.

Nixon, K.C. and J. Carpenter. 1993. On outgroups. Cladistics, 9: 413-426.

Nixon, K. C. and J. I. Davis. 1991. Polymorphic taxa, missing values and cladistic analysis. Cladistics, 7: 233-241.

O'Grady, R. T. and G. B. Deets. 1987. Coding multistate characters, with special reference to the use of parasites as characters of their hosts. Syst. Zool., 36: 268-279.

Otero, J. C. 1990. Los géneros *Micrambe* Thompson, 1863 y *Cryptophagus* Hernst, 1792 (Coleoptera: Cryptophagidae) en las Islas Canarias. Elytron, 4:137-152.

Otero, J. C. and J. A. Diaz Pazos. 1995. revision of the genus *Spaniophaenus* Reitter, 1875 (Coleoptera: Cryptophagidae). Koleopt. Rund., 65:183-188.

Pakaluk, J., Ślipiński, S. A., and J. F. Lawrence. 1995. Current classification and family-group names in Cucujoidea (Coleoptera). Genus, 5: 223-268.

Pal, T. K. and J. F. Lawrence. 1989. A new genus and subfamily of mycophagous Bothrideridae (Coleoptera: Cucujoidea) from the Indo-Australian region, with notes on related families. J. Australian Entomol. Soc. 25: 185-210.

Palm, T. 1951. Cryptophagidae. pp. 179-180 *in* Die Holz- und Rinden-Käfer der nordschwedischen Laubbäume. Meddelanden Fran Statens Skogsforskningsinstitut. Band 40.

Park, O. 1929. Taxonomic studies in Coleoptera, with notes upon certain species of beetles in the Chicago area, I. Jour. New York Entomol. Soc., 37: 429-436.

Perris, M. E. 1862. Histoire des insectes du pin maritime. Supplément aux Coléoptères et rectifications. Ann. Soc. Entomol. France, 2: 173-243, + 610 Figs.

Perris, M. E. 1877. Larves de Coléoptères. Ann. Soc. Linnéenne Lyon, 590 pp., + 14 pls.

Peterson, A. 1951. Larvae of Insects. An Introduction to Nearctic Species. Part II. Coleoptera, Diptera, Neuroptera, Siphonaptera, Mecoptera, Trichoptera. Edwards Brothers, Ann Arbor, 416 pp.

Platnick, N. I., Griswold, C. E., and J. A. Coddington. 1991. On missing entries in cladistic analysis. Cladistics, 7: 337-343.

Ponomarenko, A. G and A.B. Ryvkin. 1990. Scarabeida. pp. 39-87, + pls. 4-7 *in* A.P. Rasnitsyn, Late Mesozoic insects of eastern Transbaikalia. Nauka Press, Moscow.

Quieroz, K. de and J. Gauthier. 1990. Phylogeny as a central principle in taxonomy: Phylogenetic definitions of taxon names. Syst. Zool., 39: 307-322.

Quieroz, K. de and J. Gauthier. 1992. Phylogenetic Taxonomy. Ann. Rev. Ecol. Syst., 23: 449-480.

Ratti, E. 1976. Nota sul genere *Alfieriella* Wittmer, 1935 (=*Cyprogenia* Baudi, 1870, nec Agassiz, 1852) syn. n., con discussione sulla sua posizione sistematica. Boll. Soc. Entomol. Ital., 108: 118-122.

Reitter, E. 1875. Revision der europäischen Cryptophagiden. Deutsch. Entomol. Zeitschr., 19: 1-86.
Reitter, E. 1877a. Neue Arten aus den Familien der Cucujidae, Nitidulidae, Colydiidae und Cryptophagidae. Mitt. Münch. Entomol. Ver., 1877: 22-28.
Reitter, E. 1877b. Coleopterorum species novae. Verh. Zool-Bot. Gesell. Wien, 27: 165-194.
Reitter, E. 1879. Bestimmungs-Tabellen der europäischen Coleopteren, I. Cucujidae, Telmatophilidae, Tritomidae, Mycetaeidae, Endomychidae, Lyctidae und Sphindidae. Verh. Zool-Bot. Gesell. Wien, 29: 71-100.
Reitter, E. 1887. Bestimmungs-Tabellen der Europäischen Coleopteren. XVI Heft. Enthaltend die Familien: Erotylidae und Cryptophagidae. Troppau, Brünn, 56 pp.
Reitter, E. 1889. Zwei neue Coleopteren-Gattungen aus Transkaukasien. Wiener Entomol. Zeitung, 8: 289-292, + plt. IV.
Reitter, E. 1906. Cryptophagidae. pp. 330-337 *in* V. Heyden, E. Reitter, and J. Weise. 1906. Catalogous Coleopterorum Europae, Caucasi et Armen. Ross, Paskau.
Reitter, E. 1911. Fauna Germanica. Die Käfer des Deutschen Reiches, vol. 3. K. G. Lutz, Stuttgart, 436 pp. + plts. 81-128.
Rĕska, M. 1994. Bestimmungstabellen der mitteleuropäischen Arten der Gattungen *Micrambe* Thomson und *Cryptophagus* Herbst (Inescta: Coleoptera: Cryptophagidae). Ann. Naturhist. Mus. Wien (B) 96:247-342.
Rey, C. 1887. Essai d'etudes sur certaines larves de coléoptères. Ann. Soc. Linn. Lyon, 33: 131-256, + 2 pls.
Roff, D. 1990. The evolution of flightlessness in insects. Ecol. Mon., 60: 389-421.
Roubik, D W. and Q. D. Wheeler. 1982. Flightless beetles and stingless bees: phoresy of scotocryptine beetles (Leiodidae) on their meliponine hosts (Apidae). Jour. Kansas Entomol. Soc., 55: 125-135.
Sasaji, H. 1984. Contribution to the taxonomy of the superfamily Cucujoidea (Coleoptera) of Japan and her adjacent districts, II. Mem. Fac. Educ. Fukui Univ. Series II (Nat. Sci.), 34(2):21-63.
Scheerpeltz, O. and K. Höfler. 1948. Käfer und Pilze. Verlag für Jugend und Volk, Wien, 351 pp., + 9 pls.
Schenkling, S. 1923. Family Cryptophagidae *in* W. Junk, S. Schenkling, Coleopterorum Catalogus. Pars 76. W. Junk, Berlin, 92 pp.
Scott, H. 1935. Coleoptera associated with the giant Lobelias and arborescent Senecios of eastern Africa. Zool. Jour. Linn. Soc., 39: 235-283.
Schwarz, E.A. and H. Ulke. 1891. [Notes on *Emphylus americanus*]. Proc. Entomol. Soc. Washington, 11: 227.
Sen Gupta, T. 1967. A new subfamily of Languriidae (Coleoptera) based on four genera, with a key to the species of *Toramus*. Proc. Roy. Entomol. Soc. London (B) 36: 167-176.
Sen Gupta, T. 1968a. Review of the genera of the tribe Loberini (Coleoptera: Languriidae). Breviora, 303: 1-27.
Sen Gupta, T. 1968b. Revision of the genera of Cladoxenini (=Cladoxeninae Arrow) and Thallisellini trib. nov. of the family Languriidae (Coleoptera: Clavicornia). Jour. Nat. Hist., 2: 463-475.
Sen Gupta, T. 1969. On the taxonomy of Erotylidae [Insecta: Coleoptera: Clavicornia], with descriptions of two new larvae. Proc. Zool. Soc. Calcutta, 22: 97-107.
Sen Gupta, T. 1978. A new genus of Atomariinae (Coleoptera: Cryptophagidae) with descriptions of two new species from India. Oriental Insects, 12: 275-279.
Sen Gupta, T. and R. A. Crowson. 1966. A new family of cucujoid beetles, based on six Australian and one New Zealand genera. Ann. Mag. Nat. Hist. (13) 9: 61-85.
Sen Gupta, T. and R. A. Crowson. 1967. The systematic position of *Eicolyctus* Sahlberg (Coleoptera: Languriidae). Proc. Roy. Entomol. Soc. London (B) 36: 87-93.
Sen Gupta, T. and R. A. Crowson. 1969a. Further observations on the family Boganiidae, with definition of two new families Cavognathidae and Phloeostichidae. Jour. Nat. Hist., 3: 571-590.
Sen Gupta, T. and R. A. Crowson. 1969b. On a new family of Clavicornia (Coleoptera) and a new genus of Languriidae. Proc. Roy. Entomol. Soc. London (B) 38: 125-131.
Sen Gupta, T. and R. A. Crowson. 1971. A review of classification of the family Languriidae (Coleoptera: Clavicornia) and the place of Languriidae in the natural system of Clavicornia. Mem. Zool. Surv. India, 15(2): 1-42.
Sen Gupta, T. and T. K. Pal. 1980. Ergebnisse der Bhutan Expedition 1972 des Naturhistorischen Museum in Basel (Coleoptera: Cryptophagidae: *Henoticus*). Entomol. Basiliensia, 5: 31-41.
Setsuda, K-I. 1995. Ecological study of beetles inhabiting *Cryptoporus volvatus* (Peck) Shear (II) Relationship between development of the basidiocarps and life cycles of five major species of beetle inhabiting the fungus, with discussions of the spore dispersal. Japanese Jour. Entomol., 63:609-620.
Sjöberg, O. 1947. Die Ergebnisse einer Genitaluntersuchund der nordischen Arten der Gattung *Atomaria* Steph. (Col. Cryptophagidae). Entomol. Tidskrift, 68: 91-119.
Sharp, D. 1886. On New Zealand Coleoptera with descriptions of new genera and species. Trans. Roy. Dublin Soc., 2: 351-454, + pls. xii & xiii.
Sharp, D. and F. A. G. Muir. 1912. The comparative anatomy of the male genital tube in Coleoptera. Trans. Entomol. Soc. London, 1912: 477-642, pls. XLII-LXXVIII.
Shuckard, W. E. 1839. Elements of British Entomology, ..., part I. Hippolyte Ballière, London, 240 pp.
Ślipiński, S. A. 1990. A monograph of the world Cerylonidae (Coleoptera: Cucujoidea). Part I - Introduction and higher classification. Ann. Museo Civicio Storia Nat. Genova, 88: 1-273.
Ślipiński, S. A. and J. Pakaluk. 1991. Problems in the classification of the cerylonid series of Cucujoidea (Coleoptera). pp. 79-88 *in* M. Zunino, X. Bellés, M. Blas, Advances in Coleopterology. Silvestrelli and Cappelletto, Torino.
Spahr, U. 1981. Systematischer Katalog der Bernstein- und Kopal-Käfer (Coleoptera). Stuttgarter Beiträg. Naturk (Ser. B: Geologie und Paläontologie), No. 80: 1-107.
Stephens, J. F. 1829a. Illustrations of British Entomology .... Mandibulata, vol. II. Baldwin and Cradock, London, 200 pp. + pls. X-XV.
Stephens, J. F. 1829b. A systematic Catalogue of British Insects, Part 1. Baldwin and Cradock, London, xxxiv + 416 pp.
Stephens, J. F. 1830. Illustrations of British Entomology; .... Mandibulata, vol. III. Baldwin and Cradock, London, 374 pp. + pls. XVI-XIX.
Strand, E. 1936. Miscellanea nomenclatoria zoologica et paleontologica. Folia Zool. Hydrobiol. Riga, 9: 167-170.
Swofford, D.L. 1993. Phylogenetic Analysis Using Parsimony (PAUP), version 3.1.1. Illinois Natural History Survey, Champaign.
Swofford, D.L. and W.P. Maddison. 1987. Reconstructing ancestral character states under Wagner parsimony. Math. Biosci., 87: 199-229.
Thayer, M. 1992. Discovery of sexual wing dimorphism in Staphylinidae (Coleoptera): "*Omalium*" *flavidum*, and a discussion of wing dimorphism in insects. Jour. New York Entomol. Soc. 100: 540-573.
Thomas, M. C. 1984a. A new species of apterous *Telephanus* (Coleoptera: Silvanidae) with a discussion of phylogenetic relationships of the Silvanidae. Coleopterists Bull., 38: 43-55.
Thomas, M. C. 1984b. A new neotropical genus and species of rostrate Laemophloeinae (Coleoptera: Cucujidae) with discussion of the systematic position of the subfamily. Coleopterists Bull., 38: 67-83.
Thomson, C. G. 1863. Skandinaviens Coleoptera, Synoptiskt Bearbetade. Tom. V. Lundbergska Boktryckeriet, Lund, 340 pp.
Thomson, C. G. 1868. Skandinaviens Coleoptera, Synoptiskt Bearbetade. Tom. X. Lundbergska Boktryckeriet, Lund, 420 pp.
Verhoeff, K. W. 1923. Beiträge zur Kenntnis der Colepteren-Larven mit besonderer Berücksichtigung der Clavicornia. Arch. Naturgesch. (A), 89: 1-109, + 7 pls.

Watrous, L. E. and Q. D. Wheeler. 1981. The out-group comparison method of character analysis. Syst. Zool., 30: 1-11.
Watt, J. C. 1980. *Zeonidicola* (Coleoptera: Cavognathidae)—Beetles inhabiting birds' nests. Jour. Roy. Soc. New Zealand, 10: 331-339.
Weiss, H. B. and E. West. 1920. Fungous insects and their hosts. Proc. Biol. Soc. Washington, 33: 1-20.
Westwood, J. O. 1840. Synopsis of the Genera of British insects. pp. xi + 1-158 *in* An Introduction to the Modern Classification of Insects, Founded on the Natural Habits and Corresponding Organization of the Different Families, vol. II. Orme, Brown, Green and Longmans, London.
Wheeler, W. M. 1919. The phoresy of *Antherophagus*. Psyche, 26: 145-152.
Wiley, E.O., D. Siegel-Causey, D.R. Brooks, & V.A. Funk. 1992. The Compleat Cladist: A Primer of Phylogenetic Procedures. University of Kansas Museum Special Publications, No. 19, 158 pp.
Wittmer, W. 1935. Ein neues Genus aus der Familie der Cucujidae. Bull. Entomol. Soc. Egypte, 19: 129-131.
Wollaston, T.V. 1854. Insecta Maderensia; Being an Account of the Insects of the Islands of the Madeiran Group. J. Van Voorst, London, xlii + 634 pp.
Wollaston, T.V. 1857. Catalogue of the Coleopterous insects of Madeira in the British Museum. British Museum, London, xvi + 234 pp.
Wollaston, T.V. 1864. Catalogue of the Coleopterous insects of the Canaries, in the collection of the British Museum. British Museum, London, xiii + 648 pp.
Woodroffe, G. E. and C. W. Coombs. 1961. A revision of the North American *Cryptophagus* Herbst (Coleoptera: Cryptophagidae). Misc. Publ. Entomol. Soc. Am., 2: 179-211.
Xembeu. 1898. Moeurs et métamorphoses des insectes. 9^{e} mémoire. Rev. Entomol. [Caen], 17: 1-63.
Xembeu. 1901. Moeurs et métamorphoses des insectes. 9^{e} mémoire. Rev. Entomol. [Caen], 20: 7-68.
Xembeu. 1906. Moeurs et métamorphoses des coléoptères du groupe des mycétophagides. Naturaliste, 28: 101-103, 120-121.
Xembeu. 1907. Moeurs et métamorphoses des insectes. Ann. Soc. Linn. Lyon, 54: 109-170.
Zherichnin, V. V. 1977. Family Cryptophagidae. pp. 138-139 *in* L. V. Arnol'di, V. V. Zheriknin, L.M., Nikritin, A.G. Ponomarenko, eds., Mesozoic Coleoptera. Trudy Paleontologicheskogo Instituta, Akademiya Nauk SSSR Vol. 61, Nauka, Moscow.

APPENDIX. TAXA OF CRYPTOPHAGIDAE AND RELATED CUCUJOIDEA EXAMINED.

The following list includes taxa examined to determine character distributions in the phylogenetic analysis and to construct diagnoses and descriptions in the taxonomic treatments. The arrangement of the list does not necessarily reflect phylogenetic relationships.

Those species of Cryptosomatulini described by Broun are not represented as designated type specimens; although the original series are currently in the Broun collection at BMNH. Because the generic status of many of these species is presently unknown I have not designated lectotypes among these series pending future studies. Notes are made about possible generic placements of some species.

An asterisk (*) denotes specimens that were fully dissected and examined in glycerin or mounted on microslides. Letters following the names indicate sex of the specimens (M, male; F, female) or type material (T, Holotype; P, paratype). The general distribution of the species is indicated at the end of each entry.

Cavognathidae Sen Gupta and Crowson 1966

Cavognatha pullivora Crowson*(F), Australia
Neocercus sp., New Zealand
Taphropiestes fusca Reitter*(M), Chile
Taphropiestes sp.*(M), Brazil

Boganiidae Sen Gupta and Crowson 1966

Afroboganium sp.*(M), Africa
Paracucujus rostratus Sen Gupta and Crowson*(F), Australia

Hobartiidae Sen Gupta and Crowson 1966

Hobartius sp.*(M), Australia
Hobartius sp.*(M), Chile
Hydnobioides sp.*(M), Australia

Phloeostichidae Reitter 1911

Agapytho foveicollis Broun*(F), New Zealand
Hymaea succinifera Pascoe*(M), Tasmania
Myriabola grouvelliana Reitter*(F), Australia
Phloeostichus denticollis Reitter*(M, F), Europe
Priasilpha obscura Broun*(M), New Zealand
Rhopalobrachium sp.*(M), Chile

Cucujidae Latreille 1802

Cucujus clavipes Fabricius*(F), North America
Pediacus dermestoides Fabricius*(F), Europe
P. fuscus Erichson*(M), North America

Phalacridae Leach 1815

Cyclaxyra sp.*(M), New Zealand
Tolyphus sp.*(F), Europe
Stilbus apicalis (Melsheimer)*(M,F), North America
Phalacrinus sp.*(M), Australia

Laemophloeidae Ganglbauer 1899

Carinophloeus raffrayi (Grouvelle)*(M), Cote d'Ivoire
Metaxyphloeus germaini (Grouvelle)*(M), Central America
Laemophloeus sp. 1*(M), North America
Laemophloeus sp. 2*(M), North America
Propalticus occulatus Sharp*(M), Southeast Asia
Rhinomalus sp.*(M), Central America

Lamingtoniidae Sen Gupta and Crowson 1969

Lamingtonium bunnaburense Sen Gupta and Crowson*(F), Australia

Silvanidae Kirby 1837

Aplatamus sp.*(M), Mexico
Ahasversus sp.*(M,F), North America
Parabrontes redtenbacheri Reitter*(M), Chile
Psammoecus sp.*(M), Australia
Platamus sp.*(F), South America
Sylvanops sp.*(M), South America
Telephanus velox Haldeman*(M), North America
Uleiota dubia (Fabricius) *(M), North America

Passandridae Blanchard 1845/Erichson 1845

Scalidia linearis Leconte*(M), North America

Cryptophagidae Kirby 1837

Cryptophagini Kirby 1837

Antherophagus caucasicus Reitter, T, Europe
A. convexulus LeConte, T, North America
A. himalaicus Champion, T, Asia
A. ludekingi Grouvelle, T, Southeast Asia
A. microphthalmus Grouvelle, Southern Asia
A. nigricollis Champion, T, Asia
A. nigricornis (Fabricius)*(F), Eurasia
A. ochraceus Melsheimer*(M,F), North America
A. pallens (Fabricius), Eurasia
A. pallidivestis Casey, T, North America
Antherophagus sp. 1, Southeast Asia
Antherophagus sp. 2*(M,F), Central America
Antherophagus sp. 3, South America
Antherophagus sp. 4, South America

Asternodea loebli Leschen*(M,F), Asia

Catopochrotus crematogastri Reitter*(M), T, Europe

Cryptophagus acutangulus Gyllenhal, Holarctic
C. altaicus Bruce, Europe
C. anatolicus Bruce, Europe
C. araxicola Reitter, T, Europe
C. auropubescens Grouvelle, T, Asia
C. axillaris Reitter, T, Europe
C. baldensis Erichson, Europe
C. bimacularis Grouvelle, T, Asia
C. binotatus Grouvelle, T, Asia
C. bipedes Bruce, T, Europe
C. castanescens Grouvelle, T, Asia
C. cellaris (Scopoli), Worldwide
C. circassicus Reitter, T, Europe
C. confertus Casey, T, Holarctic
C. convexus Grouvelle, T, Europe
C. corticinus Thomson, Holarctic
C. croceus Zimmerman, North America
C. curtus Grouvelle, T, Asia
C. deceptor Grouvelle, T, Europe
C. dentatus (Herbst), Holarctic
C. difficilis Casey, T, North America
Cryptophagus sp. nr. *difficilis* Casey*(M,F), North America
C. dilatipennis Reitter, T, Europe
C. discidens Casey, T, North America
C. distinguendens Sturm, Holarctic
C. dorsaliformis Reitter, T, Eurasia
C. durus Reitter, T, Europe
C. ellipticus (Wollaston)*(M,F), T, Canary Islands
C. enormis Hisamatsu, Japan
C. erichsoni Reitter, T, Europe
C. exilicornis Grouvelle, T, Asia
C. fumatus Marsham, Europe
C. fumidulus Casey, T, North America
C. hauseri Reitter, T, Europe
C. hebes Casey, T, North America
C. hexagonalis Tournier, Holarctic
C. histricus Casey, T, North America
C. inaequalis Reitter, T, Europe
C. infuscus Grouvelle, T, Asia
C. jakowlewi Reitter, T, Europe
C. japonicus Reitter, T, Japan
C. lapidicola Reitter, T, Holarctic
C. lapponicus Gyllenhal, Holarctic
C. latangulus Reitter, T, Europe
C. laterangulus Reitter, T, Europe
C. laticollis Lucas, T, Worldwide
C. lecontei Harold, T, North America
C. lewisi Reitter, Japan
C. longiventris Grouvelle, T, Europe
C. lucifugus Falcoz, T, Europe
C. lycoperdi (Scopoli)*(F), Eurasia
C. mainensis Casey, T. North America
C. maximus Blake*(F), North America
C. micramboides Reitter*(M), T, Japan
Cryptophagus sp. nr. *micramboides* *(M), Asia
C. nitiduloides Wollaston, Canary Islands
C. obsoletus Reitter, T, Worldwide
C. opacus Reitter, T, Europe
C. opacosericeus Reitter, T, Europe
C. pallidus Sturm, Europe
C. parallelicollis Grouvelle, T, Asia
C. plenus Casey, T, North America
C. politus Casey, T, North America
C. populi Paykull, P, Europe
C. porrectus Casey, T, North America
C. posticus Reitter, T. Europe
C. postpositus J. Sahlberg, Europe
C. pseudoschmidti Woodroffe, P, Europe
C. pubescens Sturm, Europe
C. quadrimaculatus Reitter, T, Europe
C. reflexicollis Reitter, T, Europe
C. ruficornis Stephens, Europe
C. robustus Grouvelle, T, Asia
C. saginatus Sturm, Worldwide
C. scanicus (Linnaeus), Holarctic
C. scotti Bruce, T, Africa
C. setulosus Sturm, Holarctic
C. simplex Miller, Europe
C. simulator Grouvelle, T, Asia
C. skalitzkyi Reitter, T, Europe
C. spaelus Falcoz, P, Europe
C. spadiceus Falcoz, T, Europe
C. straussi Ganglbauer, P, Europe
C. subvittatus Reitter, T, Eurasia
C. thomsoni Reitter, T, Europe
C. tuberculosus Mäklin, Holarctic
C. valens Casey, T, North America
C. versicolor Lindberg, Europe
C. vicinus Grouvelle, T, Asia
Cryptophagus sp. 1*(M,F), North America

Cryptophagus sp. 2*(M), Central America
Cryptophagus sp. 3*(F), Asia

Henoticus alluaudi (Grouvelle), Africa
H. basilewskyi Bruce, T, Africa
H. bimaculosus Bruce, T, Africa
H. brevis (Grouvelle), **new combination**, T, Africa
H. burgeoni Bruce, T, Africa
H. californicus (Mannerheim)*(M,F), Worldwide
H. convexus Bruce, T, Africa
H. elgonensis Bruce, T, Africa
H. flavipennis Johnson, T, Asia
H. incertus Bruce, T, Africa
H. indicus Grouvelle, Asia
H. meruensis Bruce, T, Africa
H. minor Bruce, T, Africa
H. montanus Bruce, T, Africa
H. mycetoecus (Park)*(M), P, North America
H. productus Bruce, T, Africa
H. regificus Johnson, T, Asia
H. rhodesiensis Bruce, T, Africa
H. rotundatus Bruce, T, Africa
H. ruthae Bruce, T, Africa
H. scotti Bruce, T, Africa
H. serratus (Gyllenhal),Worldwide
Henoticus sp. 1*(M), Africa
Henoticus sp. 2*(M), Africa

Henotiderus centromaculatus Reitter*(F), Japan
H. obesulum Casey*(M,F), T, North America
(H *hirtus* Casey), **new synonymy**, T, North America
H. lorna (Hatch)*(M), North America
Henotiderus sp. 1, California
Henotiderus sp. 2, Idaho
Henotiderus sp. 3, Taiwan

Henotimorphus belovi Ljubarsky*(M), P, Asia

Micrambe abietis (Paykull)*(M,F), T, Europe
M. acerba (Bruce) **new combination**, T, Africa
M. africana (Bruce) **new combination**, T, Africa
M. alberti (Bruce) **new combination**, T, Africa
M. alluaudi (Scott), T, Africa
M. angolensis (Bruce) **new combination**, T, Africa
M. anguliformis (Bruce) **new combination**, T, Africa
M. basuto (Bruce) **new combination**, T, Africa
M. bicolorata (Bruce) **new combination**, T, Africa
M. bimaculata (Panzer), Eurasia
M. brachythoraca (Bruce) **new combination**, T, Africa
M. brevipila (Bruce) **new combination**, T, Africa
M. brincki (Bruce) **new combination**, T, Africa
M. brevitarsa (Bruce) **new combination**, T, Africa
M. bujukuensis Scott, T, Africa
M. burgeoni (Scott), T, Africa
M. caffer (Bruce) **new combination**, T, Africa
M. castanea (Bruce) **new combination**, T, Africa
M. convexa Grouvelle, T, Africa
M. crateris (Scott), T, Africa
M. defecta (Bruce) **new combination**, T, Africa
M. difficilis (Bruce) **new combination**, T, Africa
M. discolor (Bruce) **new combination**, T, Africa
M duclouxi (Grouvelle) **new combination**, T, Asia
M. eichelbaumi Grouvelle, T, Africa
M. eggelingi Scott, T, Africa
M. elgonensis (Bruce) **new combination**, T, Africa
M. figurata (Bruce) **new combination**, T, Africa
M. goliath Grouvelle, T, Africa
M. hanstromi (Bruce) **new combination**, T, Canary Islands
M. helychrisi (Scott)*(M), T, Africa
M. hesperia (Wollaston), Canary Islands
M. hirta Grouvelle, T, Africa
M. irritabilis (Bruce) **new combination**, T, Africa
M. johnstoni (Scott), T, Africa
M. kigoensis Scott, T, Africa
M. kivuensis (Bruce) **new combination**, T, Africa
M. kolbei Grouvelle, T, Africa
M. leleuporum (Bruce) **new combination**, T, Africa
M. lobeliae (Bruce) **new combination**, T, Africa
M. madagascariensis Grouvelle, T, Madagascar
M. mauritii Grouvelle, T, Africa
M. maurotis (Bruce) **new combination**, T, Africa
M. minor (Bruce) **new combination**, T, Africa
M. minuta Grouvelle, T, Africa
M. modesta Grouvelle, T, Africa
M. molesta (Bruce) **new combination**, T, Africa
M. monotrix (Bruce) **new combination**, T, Africa
M. mutilata (Bruce) **new combination**, T, Africa
M. natalensis (Bruce) **new combination**, T, Africa
M. nigerrima (Bruce) **new combination**, T, Africa
M. oblonga (Bruce) **new combination**, T, Africa
M. olkokolae (Bruce) **new combination**, T, Africa
M. opacula Grouvelle, T, Africa
M. parvicollis (Bruce) **new combination**, T, Africa
M. parvula (Bruce) **new combination**, T, Africa
M. perrisi (C. Brisout de Barneville), Europe
M. perspicua (Bruce) **new combination**, T, Africa
M. peringueyi Grouvelle, T, Africa
M. plagiata Peringuey, Africa
M. punctata Grouvelle, T, Africa
M. punctulata (Bruce) **new combination**, T, Africa
M. quadricollis (Bruce) **new combination**, T, Africa
M. reitteri Grouvelle, T, Africa
M. rufitarsis (Bruce) **new combination**, T, Africa
M. scotti (Bruce) **new combination**, T, Africa
M. senecionis Scott, T, Africa
M. simoni Grouvelle, T, Africa
M. similis (Bruce) **new combination**, T, Africa
M. solitaria (Bruce) **new combination**, T, Africa
M. singularis (Bruce) **new combination**, T, Africa
M. subinfuscata Grouvelle, P, Africa
M. subvillosa Grouvelle, T, Africa
M. tanganyikae (Bruce) **new combination**, T, Africa
M. tenebrata (Bruce) **new combination**, T, Africa
M. turneri (Bruce) **new combination**, T, Africa
M. varicolor (Bruce) **new combination**, T, Africa
M. vini (Panzer), Europe
Micrambe sp. 1*(M,F), Madagascar
Micrambe sp. 2*(F), Africa
Micrambe sp. 3*(F), Africa
Micrambe sp. 4*(M), Africa

Mnionomidius serricollis (Reitter)*(M), Europe

Mnioticus hancocki (Scott)*(M,F), T, Africa
M. gibbinsi (Scott), T, Africa
M. jeanneli (Scott), T, Africa
M. rhyncopelati (Scott), T, Africa
Mnioticus sp. 1*(M), Africa
Mnioticus sp. 2*(M,F), Africa

Myrmedophila americana (LeConte)*(M,F), North America

Neohenoticus palmerae Leschen*(M,F), Chile

Paramecosoma melanocephalum (Herbst)*(M,F), Eurasia

Pteryngium crenatum (Fabricius)*(M,F), Holarctic

Salebius lictor Casey, T, North America
S. minax Casey, T, North America
Salebius sp. nr. *minax*(M,F), North America
S. octodentatus (Mäklin), North America
S. tarsalis Casey, T, North America

Serratomaria tarsalis Nakane and Hisamatsu*(M), Japan
S. vulgaris Sasaji*(M,F), P, Japan
Serratomaria sp. 1*(M), Asia
Serratomaria sp. 2, Asia
Serratomaria sp. 3, Asia

Spaniophaenus caucasicus Reitter*(M), T, Europe
S. lapidarius (Fairmaire), Europe
S. laticollis (Miller)*(M), Europe

Spavius glaber Motschulsky*(M,F), Europe

Striatocryptus wilkinsoni Leschen*(M), Asia
S. polyglandis Leschen*(M), Asia
Striatocryptus sp. 1*(F), India
Striatocryptus sp. 2, Vietnam
Striatocryptus sp. 3, Uganda
Striatocryptus sp. 4, Thailand
Striatocryptus sp. 5, India
Striatocryptus sp. 6, India

Telmatophilus americanus LeConte*(M,F), North America
T. bicolor Reitter, T, Europe
T. caricis (Olivier)*(M,F), Eurasia
T. typhae (Fallén)*(F), Europe
T. sparganii (Ahrens), Eurasia
Telmatophilus sp.*(F), unknown

Genus 1 sp. 1, M, Kenya

Cryptosomatulini Crowson 1980

Agnetaria cryptophagoides Bruce*(F, M), T, South Australia

Antarcticotectus aucklandicus Brookes, T, New Zealand
Antarcticotectus sp. 1*(M,F), New Zealand

Brounina distincta (Broun), T, New Zealand
Brounina fossulata Bruce, Chile
Brounina sp. 1*(M), Chile
Brounina sp. 2*(M,F), Chile
Brounina sp. 3*(F), Chile

Chiliotis exilis Grouvelle, T, Chile
C. formosa Reitter, Chile
C. germaini Grouvelle, T, Chile
C. gigas Grouvelle, T, Chile
C. gracilis Grouvelle, T, Chile
C. laticeps Grouvelle, T, Chile
C. longicornis Grouvelle, T, Chile
Chiliotis sp. 1, Trinidad
Chiliotis sp. 2, Ecuador
Chiliotis sp. 3*(F), Australia
Chiliotis sp. 4*(M,F), Australia
Chiliotis sp. 5*(M), Chile
Chiliotis sp. 6*(M,F), Chile
Chiliotis sp. 7, Australia

Cryptosomatula longicornis Bruce, T, Juan Fernandez Islands

Cryptophagus gibbipennis Blackburn, T, Australia (member of an undescribed genus)
Cryptophagus sp. 1 nr. *gibbipennis*(F), Australia
Cryptophagus sp. 2 nr. *gibbipennis*(M,F), Australia
Cryptophagus sp. 3 nr. *gibbipennis*(F), Australia
C. lindensis Broun, T, New Zealand (probably a member of *Chiliotis*)
C. nigroapicalis Blackburn, T, Australia (probably a member of *Micrambina*)
C. tasmanicus Blackburn, T, Australia (member of an undescribed genus)
Cryptophagus sp. nr. *tasmanicus*(M,F), New Zealand

Cryptothelypterus atomaroides (Grouvelle), **new combination**, T, Chile
C. obrieni Leschen and Lawrence*(M,F), T, Juan Fernandez Islands
C. pteropilosus Leschen and Lawrence, T, Juan Fernandez Islands

C. selkirki (Bruce)*(M), T, Juan Fernandez Islands
C. skottsbergi (Bruce), T, Juan Fernandez Islands
C. splendens (Bruce), T, Juan Fernandez Islands

Micrambina basalis Grouvelle*(MF), T, Chile
M. discoidea (Broun), New Zealand
M. distincta (Broun), New Zealand
M. helmsi (Reitter)*(M,F), New Zealand
M. insignis Reitter, New Zealand
M. obscura (Broun), New Zealand
M. rutila (Broun), New Zealand
M. silvana (Broun), New Zealand (probably a member of *Antarcticotectus*)
M. tumida (Broun), New Zealand (member of an undescribed genus)
Micrambina sp. 1*(M,F), New Zealand
Micrambina sp. 2, Australia

Neopicrotus peckorum Leschen*(M), Chile

Picrotus thoracicus Sharp*(M,F), T, New Zealand
(*Picrotus pensus* Broun), **new synonomy**, New Zealand
(*Picrotus sanguineus* Broun), **new synonomy**, New Zealand
Picrotus sp. 1*(M,F), New Zealand

Thortus ovalis Broun*(F), T, New Zealand
Thortus sp. 1, New Zealand (labeled as *Pithortus* in the Broun Collection)
Thortus sp. 2*(M), New Zealand
Thortus sp. 3*(M, F), New Zealand

Genus 2 sp. 1*(M,F), New Zealand

Genus 3 sp. 1*(F), Australia

Caenoscelini Casey 1900

Caenoscelis antennalis (Casey)*(M,F), T, North America
C. cryptophaga Reitter*(M,F), Holarctic
C. ferruginea (Sahlberg),T, Holarctic
C. fleischeri Reitter, Europe
C. optata Sharp, T, Central America
C. sibirica Reitter, T, Eurasia
C. subdeplanata C. Brisout de Barneville, Holarctic
Caenoscelis sp. 1, Africa
Caenoscelis sp. 2, Asia
Caenoscelis sp. 3, Asia

Dernostea tanakai Sasaji*(F), P, Japan

Himascelis kashmirensis Sen Gupta and Pal, Asia
H. nigratus Sen Gupta, P, Asia
Himascelis sp. 1*(F), Nepal
Himascelis sp. 2*(M), Pakistan

Sternodea baudii Reitter, Europe
S. dichroa Reitter, P, Europe
S. lederi Reitter, Reitter
S. miki Reitter, P, Europe
S. raddei Reitter, Europe
Sternodea sp. 1*(M,F), Mexico
Sternodea sp. 2*(M,F), Mexico

Hypocoprini Reitter 1879

Alfieriella denticulata (Baudi)*(M), P, Europe
A. laticollis (Reitter), Europe
A. naxiana (Reitter), Europe
A. rabinovitchi Wittmer, Europe
Alfieriella sp. 1*(F), India

Amydropa anophthalma Reitter*(F), Chile
A. clarki Leschen*(M,F), Mexico

Hypocoprus lathridioides Motschulsky*(F), Eurasia
H. tenuis Casey* (M,F), T, North America

Atomariini LeConte 1861

Atomaria subgenus *Anchicera*

Atomaria alternans Wollaston*(M), Canary Islands
A. analis Erichson*(F), Europe
A. apicalis Erichson, Europe
A. atricapilla Stephens, Europe
A. attila Reitter, Europe
A. basalis Erichson, Eurasia
A. chillaloensis Scott, Africa
A. fasciata Kolenati*(M), Eurasia
A. fuscata (Schönherr)*(M), Holarctic
A. fuscipes (Gyllenhal), Europe
A. gibbula Erichson*(M), Eurasia
A. grandicollis Brisout de Barneville, Europe
A. gravidula Erichson, Europe
A. gutta Newman, Europe
A. hislopi Wollaston, Europe
A. horridula Reitter, Asia
A. jonica Reitter, Europe
A. kamtschatica Motschulsky, Holarctic
A. lewisi Reitter*(M,F), Worldwide
A. mesomela (Herbst), Europe
A. morio Kolenati, Holarctic
A. munda Erichson, Eurasia
A. nigripennis (Kugelann), Europe
A. nitidula (Marsham), Europe
A. ornata Heer, Europe
A. pallidipennis Holdhaus, Europe
A. peltata Kraatz, Eurasia
A. peltataeformis Sjöberg*(M), Europe
A. phicata Reitter, Europe
A. pusilla (Paykull)*(F), Holarctic
A. rhenana Kraatz, Europe
A. rubella Heer*(F), Europe
A. rubricollis Brisout de Barneville, Eurasia
A. scutellaris (Motschulsky), Europe
A. semitestacea Reitter, Eurasia
A. semusta Johnson, Europe
A. slavonica Johnson, Europe
A. soedermani Sjöberg, Eurasia
A. testacea Stephens, Holarctic
A. turgida Erichson, Eurasia
A. unifasciata Erichson, Europe
Atomaria sp.*(M,F), North America

Atomaria subgenus *Atomaria*

Atomaria affinis F. Sahlberg, Europe
A. alpina Heer, Europe
A. atrata Reitter, Eurasia
A. badia Erichson, Europe
A. barani Brisout de Barneville, Eurasia
A. bella Reitter, Europe
A. bescidica Reitter, Europe
A. diluta Erichson, Europe
A. fimetarii (Fabricius), Holarctic
A. impressa Erichson, Europe
A. nigrirostris Stephens*(M), Europe
A. pulchra Erichson, Holarctic
A. subangulata J. Sahlberg, Eurasia
A. trapeziformis Johnson*(F), Asia
A. umbrina (Gyllenhal), Europe
A. wollostoni Sharp, Europe
Atomaria sp.*(M,F), North America

Atomaroides ussurica (Ljubarsky)*(M), Asia

Curelius dilutus (Reitter), Eurasia
C. exiguus (Erichson)*(M,F), Europe
C. japonicus (Reitter)*(M,F), Worldwide

Chilatomaria australis (Blackburn)*(M) **new combination**, T, Australia
C. hillersae Leschen*(M,F), Chile
C. lindensis (Blackburn) **new combination**, T, Australia
Chilatomaria sp 1*(F), Chile
Chilatomaria sp. 2, Chile
Chilatomaria sp. 3*(F), Argentina
Chilatomaria sp. 4, Brasil
Chilatomaria sp. 5*(M), Australia

Ephistemus apicalis LeConte, T, North America
E. globulus (Paykull)* (M,F), Worldwide
E. perminutus Casey, T, North America
E. splendens Johnson, T, Asia
E. distans Erichson, Central America
Ephistemus sp. 1*(M), Costa Rica
Ephistemus sp. 2, Bolivia

Microatomaria hintoni Leschen*(M,F), Australia, New Guinea

Ootypus globosus (Waltl)*(M,F), Europe

Paratomaria crowsoni Leschen*(M,F), New Zealand

Salltius rufipes (Broun)*(M,F), T, New Zealand

Tisactia subglabra Casey*(M,F), T, North America
Tisactia sp. 1*(M), North America
Tisactia sp. 2, North America
Tisactia sp. 3, Mexico

Cryptafricini Leschen

Cryptafricus leleupi Leschen*(M), Africa

Cryptogasterus lawrencei Leschen*(M,F), Australia

Anitamaria thayerorum Leschen*(M,F), Australia
Anitamaria sp. 1, Ghana
Anitamaria sp. 2*(M), Costa Rica
Anitamaria sp. 3*(F), Costa Rica
Anitamaria sp. 4*(M,F), Australia
Anitamaria sp. 5*(F), South Africa
Anitamaria sp. 6*(M), Ivory Coast
Anitamaria sp. 7*(M,F), Nepal
Anitamaria sp. 8, Uganda
Anitamaria sp. 9, Uganda

Microphagus johnsoni Leschen*(M), Ecuador
Microphagus sp. 1*(F), Panama
Microphagus sp. 2, Peru
Microphagus sp. 3*(F), Costa Rica

ANNOUNCEMENT

The *University of Kansas Science Bulletin* (continuation of the *Kansas University Quarterly*) is an outlet for scholarly scientific investigations carried out at the University of Kansas or by University faculty and students. Since its inception, volumes of the *Bulletin* have been variously issued as single bound volumes, as two or three multi-paper parts or as series of individual papers. Issuance is at irregular intervals, with each volume prior to volume 50 approximately 1000 pages in length. Effective with volume 50, page size has been enlarged, reducing the length of each volume to about 750 pages.

The supply of all volumes of the *Kansas University Quarterly* is now exhausted. However, most volumes of the *University of Kansas Science Bulletin* are still available and are offered, in exchange for similar publications, to learned societies, colleges and universities and other institutions, or may be purchased at $30.00 per volume. Where some of these volumes were issued in parts, individual parts are priced at the rate of 3 cents per page. Current policy, initiated with volume 46, is to issue individual papers as published. Such separata may be purchased individually at the rate of 7 cents per page, with a minimum charge of $1.50 per separate. Subscriptions for forthcoming volumes may be entered at the rate of $30.00 per volume. All communications regarding exchanges, sales and subscriptions should be addressed to the EXCHANGE LIBRARIAN, UNIVERSITY OF KANSAS LIBRARIES, LAWRENCE, KANSAS 66045.

Reprints of individual papers for personal use by investigators are available for most recent and many older issues of the *Bulletin*. Such requests should be directed to the author.

The International Standard Serial Number of this publication is US ISSN 0022-8850.

Editor
Charles D. Michener

Editorial Board
Meredith Lane, *Chairman*
James S. Ashe
George W. Byers
Christopher Haufler
Norman A. Slade

THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. 55, No. 16, pp. 635-692 November 1, 1996

LIBRARY
JAN 06 1997
HARVARD UNIVERSITY

Phylogenetic Analysis and Taxonomic Revision of the *Perdita* Subgenera *Macrotera*, *Macroteropsis*, *Macroterella* and *Cockerellula* (Hymenoptera: Andrenidae)[1]

BRYAN N. DANFORTH[2]

TABLE OF CONTENTS

Abstract 635
Introduction 638
Materials, Methods and Terminology 638
Phylogenetic Relationships among the *Perdita* Subgenera 639
Species Chosen for Preliminary Analysis 639
Data Matrix 640
Character Descriptions 640
Phylogenetic Analysis 648
Monophyly of *Perdita* 649
Relationships among the *Perdita* Subgenera 649
Placement of the Subgenus *Xeromacrotera* 654
Phylogenetic Relationships among Species in the *Macrotera* Group of Subgenera 654
Data Matrix 654
Character Descriptions 654
Phylogenetic Analysis 658
Tree Topology and Relationships among Species 658
Classification 660
Diagnosis of the *Macrotera* Group of Subgenera 660
Key to the Species of the *Macrotera* Group 661
Species Diagnoses 663
Subgenus *Macroterella*, 663; Subgenus *Macrotera*, 669; Subgenus *Macroteropsis*, 669; Subgenus *Cockerellula*, 678; Subgenus *Heteroperdita*, 691
Acknowledgments 691
Literature Cited 691

ABSTRACT

This paper presents a preliminary phylogenetic analysis of the 21 *Perdita* subgenera based on internal and external morphological characters. Based on this analysis, the genus *Perdita* is clearly monophyletic. The analysis yielded 6 equally parsimonious trees; a central polytomy, involving 7 groups, is the greatest source of ambiguity. These results provide the basis for a species-level phylogenetic analysis of the monophyletic group of 31 species included in the subgenera *Macrotera*, *Macroteropsis*, *Cockerellula*, and *Macroterella*. This group (referred to as the *Macrotera* group of subgenera) forms the sister group to the remaining species in the genus. Phylogenetic analysis resulted in 4 equally parsimonious trees. The greatest source of ambiguity involves the relationships among the basal species in the clade. Classificatory changes in the limits of these subgenera are made as a consequence of the species-level analysis.

[1] CONTRIBUTION NUMBER 3183 FROM THE SNOW ENTOMOLOGICAL DIVISION, NATURAL HISTORY MUSEUM, UNIVERSITY OF KANSAS, LAWRENCE.
[2] PRESENT ADDRESS: DEPARTMENT OF ENTOMOLOGY, COMSTOCK HALL, CORNELL UNIVERSITY, ITHACA, NY 14853

Plate I. Small-headed male of *Perdita portalis*.

MCZ
LIBRARY
JAN 06 1997
HARVARD
UNIVERSITY

Plate II. Large-headed male of *Perdita portalis.*

INTRODUCTION

The genus *Perdita* contains numerous species of small to minute bees which are most abundant in the arid southwestern U.S. and northern Mexico but range across the United States, northward to southern Canada and as far south as Guatemala. The genus was first described by Smith in 1853 based on specimens of *Perdita halictoides* in the British Museum. Since then over 500 species have been described, the vast majority of them by P.H. Timberlake (1953-1980). Since Timberlake's revisions little work has been done on the genus and especially lacking is a phylogenetic analysis of this large genus of bees. The present work is meant as a first step in the phylogenetic analysis of the group. First, a phylogenetic hypothesis for the *Perdita* subgenera is proposed based on an investigation of representative species from all 21 subgenera. The preliminary analysis reveals the existence of a basal lineage of four subgenera (*Macrotera, Macroteropsis, Cockerellula* and *Macroterella;* herein called the *Macrotera* group). The second part of this study focuses on the evolutionary relationships among the 31 included species.

This work is meant to complement recent work on the behavior and morphology of several species of *Perdita* (Danforth, 1989b; Danforth, 1991a,b; Neff & Danforth, 1992, Danforth & Neff, 1992; Norden, et al., 1992).

MATERIALS, METHODS AND TERMINOLOGY

Many external morphological features were used in this study and some of these characters were easily visible in pinned specimens. However, internal morphological structures and characters of the mouthparts and terminal metasomal segments could only be seen in cleared, disarticulated specimens. Specimens were cleared in a weak solution of potassium hydroxide for one to two days and then repeatedly rinsed in distilled water. Cleared specimens were then stored in glycerol in plastic, 24-well tissue culture dishes. In order to see some characters in naturally pale or overly cleared sclerites it was necessary to stain the cuticle with a dilute solution of acid fuchsin.

The morphological terminology used follows that of Michener (1944), and other authors (Eickwort, 1969; Brooks, 1988). Terms used to describe surface sculpturing follow Harris (1979). Unlike Michener (1944), but as in his recent works, I have called the sternum and tergum of the first metasomal segment (homologous to the second abdominal segment) tergum 1 (abbreviated T1) and sternum 1 (abbreviated S1), respectively. The following metasomal sclerites are numbered sequentially thereafter (Fig. 1a). Terga (Fig. 1b,d) possess paired muscle attachment sites, termed apodemes, graduli, extending nearly the width of the tergum, and laterally, the paired spiracles (Fig. 1d). Sterna possess apodemes also, but, in *Perdita*, lack graduli (Fig. 1c).

In males there are seven visible terga and eight sterna, although S8 is occasionally retracted (Fig. 1a). T8 is visible only as a weakly sclerotized structure bearing apical setae on the internal surface of T7. S8 can be divided into a region proximal of the apodemal arms, the disc, and a region distal to the apodemes, the apex (Fig. 1e). S7 and S8 are highly variable in shape and are important characters for species identification.

In females there are 6 visible terga and sterna. S6 is highly variable and often useful for identifying females to species (Fig. 1f).

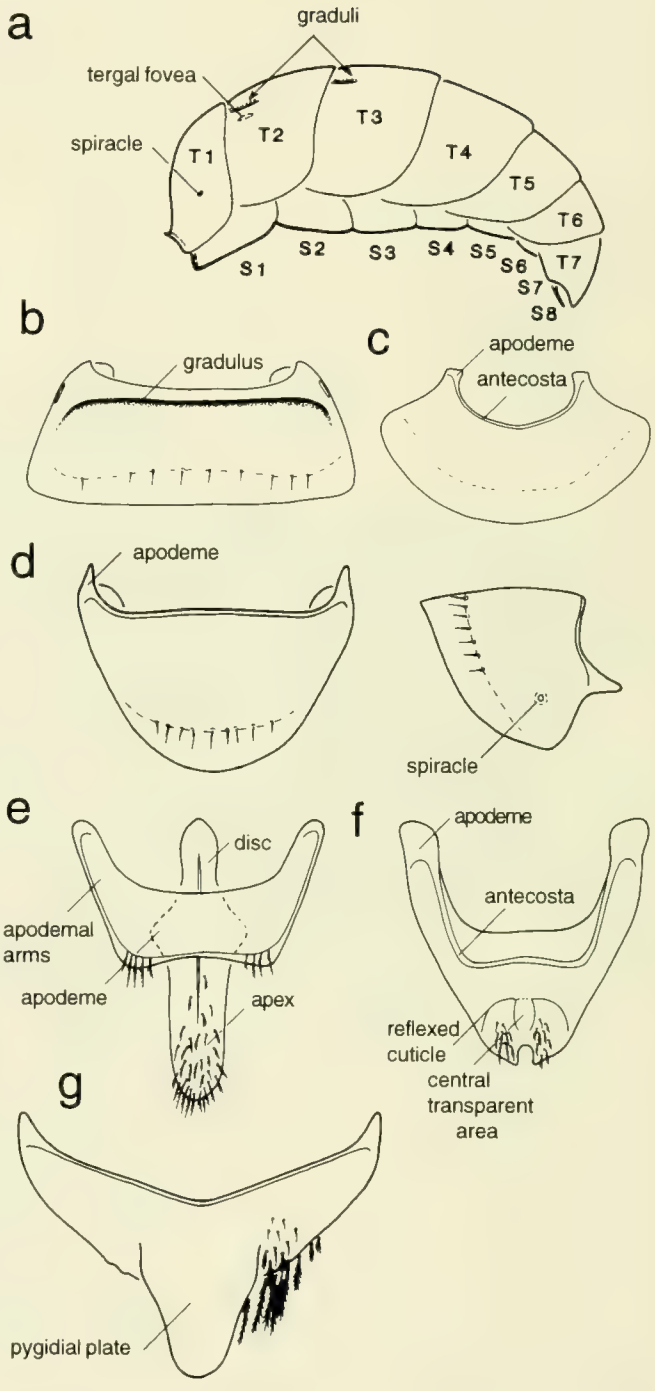


Fig. 1. Morphology of the metasoma in *P. texana:* **(a)** lateral view of male metasoma showing numbering of terga and sterna, **(b)** dorsal view of male second sternum, **(c)** ventral view of male second tergum, **(d)** dorsal and lateral views of male sixth tergum, **(e)** ventral view of male S7 and S8, **(f)** ventral view female S6, **(g)** dorsal view female T6, showing pygidial plate.

The sixth tergum in females bears the pygidial plate (Fig. 1g). The sting in *Perdita* is very weakly developed and was not studied in detail. Anteriorly the female S6 bears apodemal arms, like the preceding sterna. On the inner surface of the sterna, connecting the apodemal arms is a thickened bar of cuticle termed the antecosta (Michener, 1944). On S6 the antecosta often is separated from the anterior margin of the sterna, and can show variability between species in its shape and path. Apically, S6 often bears a thickened pad of cuticle on its internal surface, termed here the reflexed cuticle, which is highly variable in shape. In most species the reflexed cuticle is fused to the outer layer of cuticle forming a central transparent area (Fig. 1f).

The male genitalia are highly variable among species of *Perdita*. The genital capsule consists of large gonocoxites, which in some species, give rise apically to gonostyli. Ventrally one sees the paired, clasper-like volsellae. Each volsella consists of a larger, ventral cuspis which arises from the basivolsella and the smaller, dorsal digitus (Snodgrass, 1941). In *Perdita* the cuspis bears few to many papillae on its upper surface and the digitus usually has a few papillae also. Within the genital capsule is the elongate aedeagus, or penis, consisting of lateral sclerotized penis valves which, in some species, are fused into a single tube-like structure, or in others, remain separate lateral sclerites of the aeadagus. The apodemal arms of the aedagus are variable in shape, from elongate and straight to dorsally reflexed. The aedeagus sometimes contains useful characters and for this reason I have illustated the aedeagus and genital capsule separately.

Analyses of the data matrices were performed using the computer program Hennig86, version 1.5 (Farris, 1988; but see also Fitzhugh, 1989; and Platnick, 1990).

PHYLOGENETIC RELATIONSHIPS AMONG THE *PERDITA* SUBGENERA

Species Chosen for Preliminary Analysis

The species used for the preliminary analysis of the higher level relationships within the genus were selected based on Timberlake's (1954-1980) concepts of the subgenera (Table 1). At least one species was studied in detail from each of the 21 subgenera and, in some cases, more species were examined in order to evaluate the monophyly of each subgenus. The species studied in detail are listed below according to subgenus. Effort was made to examine the type species of each subgenus, but in some cases type species were poorly represented in collections and therefore could not be studied in detail. Type species which could not be examined are included in parentheses below.

ALLOMACROTERA Timb. – *P. stephanomeriae* Timb. (type species); *ALLOPERDITA* Viereck – *P. mitchelli* Timb. (*P. novaeangliae* Viereck, type species); *CALLOMACROTERA* Timb. – *Perdita maritima* Timberlake (type species); *COCKERELLIA* Ashm. – *P. albipennis albipennis* Cress., *P. albipennis heliophila* Ckll., *P. baileyae* Ckll., *P. beata beata* Ckll., *P. bequaerti indianensis* Ckll., *P. coreopsidis coreopsidis* Ckll., *P. incana* Timb., *P. lepachidis lepachidis* Ckll., *P. lingualis* Ckll., *P. obscuripennis* Timb., *P. perpulchra perpulchra* Ckll., *P. purpurascens* Timb., *P. scopata* Timb., *P. tricincta* Timb., *P. utahensis* Ckll., *P. verbesinae* Ckll. (*P. hyalina* Cress., type species); *COCKERELLULA* Timb. – *P. laticauda* Timb. (*Perdita opuntiae* Ckll., type species); *EPIMACROTERA* Timb. – *P. ainsliei* Crawford (type species), *P. diversa* Timb., *P. euphorbiae* Timb., *P. nanula* Timb., *P. parvula* Timb.; *GLOSSOPERDITA* Ckll. – *P. blaisdelli* Timb., *P. giliae* Timb., *P. hurdi* Timb., *P. navarretiae* Timb., *P. pelargoides* (Ckll.) (type species); *HESPEROPERDITA* Timb. – *Perdita ruficauda ruficauda* Ckll. (type species); *HETEROPERDITA* Timb. – *P. arenaria* Timb., *P. bellula* Timb., *P. coldeniae* Timb., *P. rhodogastra* Timb. (type species), *P. scutellaris* Timb., *P. sexfasciata* Timb., *P. trifasciata* Timb., *P. wasbaueri* Timb.; *HEXAPERDITA* Timb. – *P. asteris* Timb., *P. bishoppi planorum* Timb., *P. boltoniae chrysopsina* Timb., *P. callicerata* Timb., *P. cambarella platyura* Ckll., *P. cara* Timb., *P. foveata foveata* Timb., *P. georgica* Timb., *P. heterothecae* Ckll., *P. ignota ignota* Ckll. (type species), *P. nubila* Timb., *P. pratti* Ckll., *P. xanthismae* Ckll.; *MACROTERA* F. Smith – *P. texana* (Cress.), *P. bicolor* (Smith) (type species); *MACROTERELLA* Timb. – *P. mellea* Timb., *P. nigrella* Timb. (*Perdita mortuaria* Timb., type species); *MACROTEROPSIS* Ashmead – *P. latior* Ckll. (type species); *PENTAPERDITA* Ckll. & Porter – *P. albovittata* Ckll. (type species), *P. amoena* Timb., *P. bradleyana* Timb., *P. chrysophila chrysophila* Ckll., *P. coahuilensis* Timb., *P. melanochlora* Ckll., *P. nigrifacies* Timb., *P. nigriviridis* Timb.; *PERDITELLA* Ckll. – *P. minima* Timb., *P. cladothricis* Ckll., *P. larreae* Ckll. (type species); *PROCOCKERELLIA* Timb. – *P. albonotata* Timb. (type species); *PSEUDOMACROTERA* Timb. – *P. turgiceps* Timb. (type species); *PYGOPERDITA* Timb. – *P. californica*

Table 1. List of *Perdita* subgenera and species groups based on Timberlake (1954-1980) and subsequent work, and numbers of valid species names (subspecies not counted). Numbers in parentheses give the number of species based on changes resulting from the present work.

Perdita subgenera	no. species
Allomacrotera	2
Alloperdita	7
Callomacrotera	2
Cockerellia	25
Cockerellula	9 (13)
Epimacrotera	21
Glossoperdita	5
Hesperoperdita	2
Heteroperdita	13 (14)
Hexaperdita	26
Macrotera	5 (6)
Macroteropsis	12 (6)
Pentaperdita	15
Perdita	
Halictoides Group	12
Octomaculata Group	111
Sphaeralceae Group	191
Ventralis Group	66
Zonalis Group	53
Valida Group	1
unplaced species	14
Perditella	5
Procockerellia	4
Pseudomacrotera	1
Pygoperdita	40
Xeromacrotera	1
Xerophasma	2
Total species	653 (651)

(Cress.), *P. interrupta* Cress. (type species); *XEROMACROTERA* Timb. – *Perdita cephalotes* (Cress.) (male only; type species); *XEROPHASMA* Ckll. – *P. bequaertiana* Ckll. (type species).

The subgenus *PERDITA* contains over half the species in the genus (Table 1). Representative species of each of Timberlake's five "groups" of *Perdita* s. str. were included in the detailed study: ZONALIS group – *P. zonalis zonalis* Cress.; HALICTOIDES group – *P. halictoides* Smith; OCTOMACULATA group – *P. octomaculata* (Say); VENTRALIS group – *P. wootonae* Ckll.; SPHAERALCEAE group – *P. sphaeralceae notata* Timb.

Character polarity was determined using the outgroup criterion (Lundberg, 1972; Watrous & Wheeler, 1981; and Maddison et al., 1984). Outgroup taxa were chosen based on Ruz's phylogeny of the panurgine genera (Fig. 2; Ruz, 1991), and included the following species: Calliopsini – *Calliopsis* (*Calliopsis*) *andreniformis* Smith, *C.* (*Calliopsima*) *coloradensis* Crawford, *C.* (*Verbenapis*) *nebraskensis* Crawford, *C.* (*Nomadopsis*) *linsleyi* Rozen, *C.* (*N.*) *scutellaris* (Fowler), *Callonychium mandibulare* Friese, *C. flaviventre* (Friese), *Acamptopoeum prinii* (Holmberg), *Arhysosage flava* Moure, *Spinoliella rufiventris* Toro; Melitturgini – *Melitturga clavicornis* Latreille; Panurgini – *Panurginus occidentalis* Crawford, *Epimethea kuznetzovi* Ckll.; Protandrenini – *Pterosarus albitarsus* (Cress.), *Heterosarus illinoensis* (Cress.).

Specimens for the subgeneric analysis came primarily from the Snow Entomological Museum, University of Kansas, but specimens were borrowed from other North American institutions listed in Acknowledgements.

DATA MATRIX

The data matrix used in this analysis is shown in Table 2. The codings for the ancestral taxon are based on consideration of all the panurgine outgroups listed. When the character states varied among outgroups, the most parsimonious hypothesis for the primitive condition in *Perdita* was chosen based on the rationale described in Watrous & Wheeler (1981). Terminal taxa included all the *Perdita* subgenera. The subgenus *Glossoperdita* was divided into two groups, the majority of *Glossoperdita* and *P.* (*Glossoperdita*) *hurdi*, because *P. hurdi* is distinct from the remainder of the subgenus *Glossoperdita* in several characters. Similarly, *Cockerellia* was broken up into the majority of *Cockerellia* species and *P.* (*Cockerellia*) *baileyae*, because *P. baileyae* lacks some of the derived characters present in the remainder of *Cockerellia*. The two groups of *Pygoperdita*, the Californica and the Interrupta groups, were treated separately, in order to test the monophyly of the subgenus.

Table 2. Data Matrix for characters of *Perdita* subgenera and species groups.

Character numbers	0000000001111111111222222222233 3
	1234567890123456789012345678901 2
ANCESTOR	0000000000000000000000?000000000
ALLOPERDITA	1011110000201100000011011011121 2
CALLOMACROTERA	1001122100212102120021010001121 2
COCKERELLIA	1001132100222112011011010101121 2
COCKER. BAILEYAE	1001132100122112011011010001121 2
ALLOMACROTERA	1201122110?221020110?1???0011?1?
COCKERELLULA	0000000001000000000000010001110 0
EPIMACROTERA	1000101010100100000010011001120 1
GLOSSOPERDITA	1000?000101001020000100110011212
P. HURDI	1001101010100100000010011001120 1
HESPEROPERDITA	1000101010101101000010011001121 1
HETEROPERDITA	1001?01010?021000000?0011001120?
HEXAPERDITA	10?112211021?102000011011101121 2
MACROTERA	0000000001000000000000010001110 0
MACROTERELLA	0000000001000000000000010001111 1
MACROTEROPSIS	0000000001000000000000010001110 0
PENTAPERDITA	1101122?10?2?1020?00110100011212
PERDITA	
HALICTOIDES GR.	1200100010102100000010011001121 2
OCTOMACULATA GR.	1000110110102100000010011001121 2
SPHAERALCEAE GR.	1001110110100100000011011001111 2
VENTRALIS GR.	1011100000200100000011010001121 2
ZONALIS GR.	1001120110102100000011011001121 2
PERDITELLA	1001000010100100000011011001121 2
PROCOCKERELLIA	1101132110222112011011010001121 1
PSEUDOMACROTERA	0000110000000000200010110001101 0
PYGOPERDITA	
CALIFORNICA GR.	1000120010100000000110010001121 0
INTERRUPTA GR.	1000120010100000000110010001121 0
XEROPHASMA	0001100000100000000011011011121 2
XEROMACROTERA	?001122??02?2?0?0??0?1???00???1?

When the plesiomorphic state of a character could be unambiguously determined based on outgroup comparison, the state was coded 0. For those characters that could not be polarized the ancestral character state was coded as unknown (? in the data matrix). Among in-group taxa, characters for which the states are not known, or which are variable within a taxon, are coded as unknown. Comments are given along with the character descriptions indicating how polarity decisions were made.

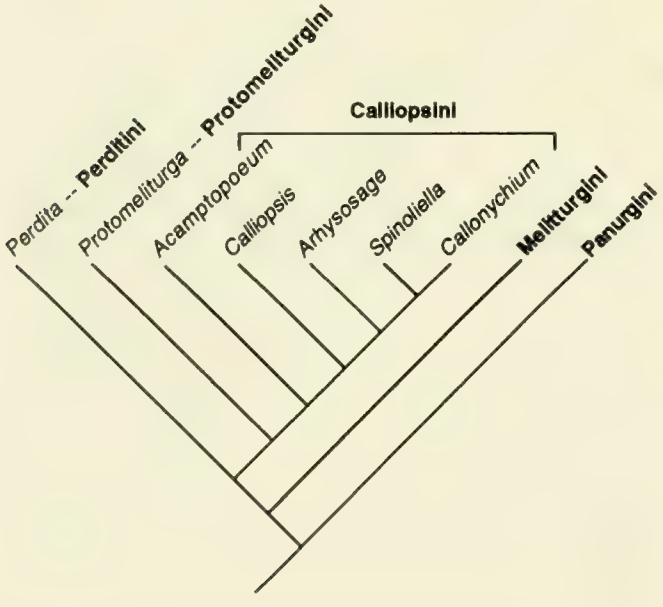


Fig. 2. Phylogeny of the Panurginae, based on Ruz (1987), showing placement of *Perdita* and relationships among outgroup taxa used.

CHARACTER DESCRIPTIONS

1(0) Female paraglossa slender basally but broadening apically to form broad, brush-like apex (Fig. 3a-c); **(1)** paraglossa slender and acutely pointed to moderately broad and parallel-sided (Fig. 3d).

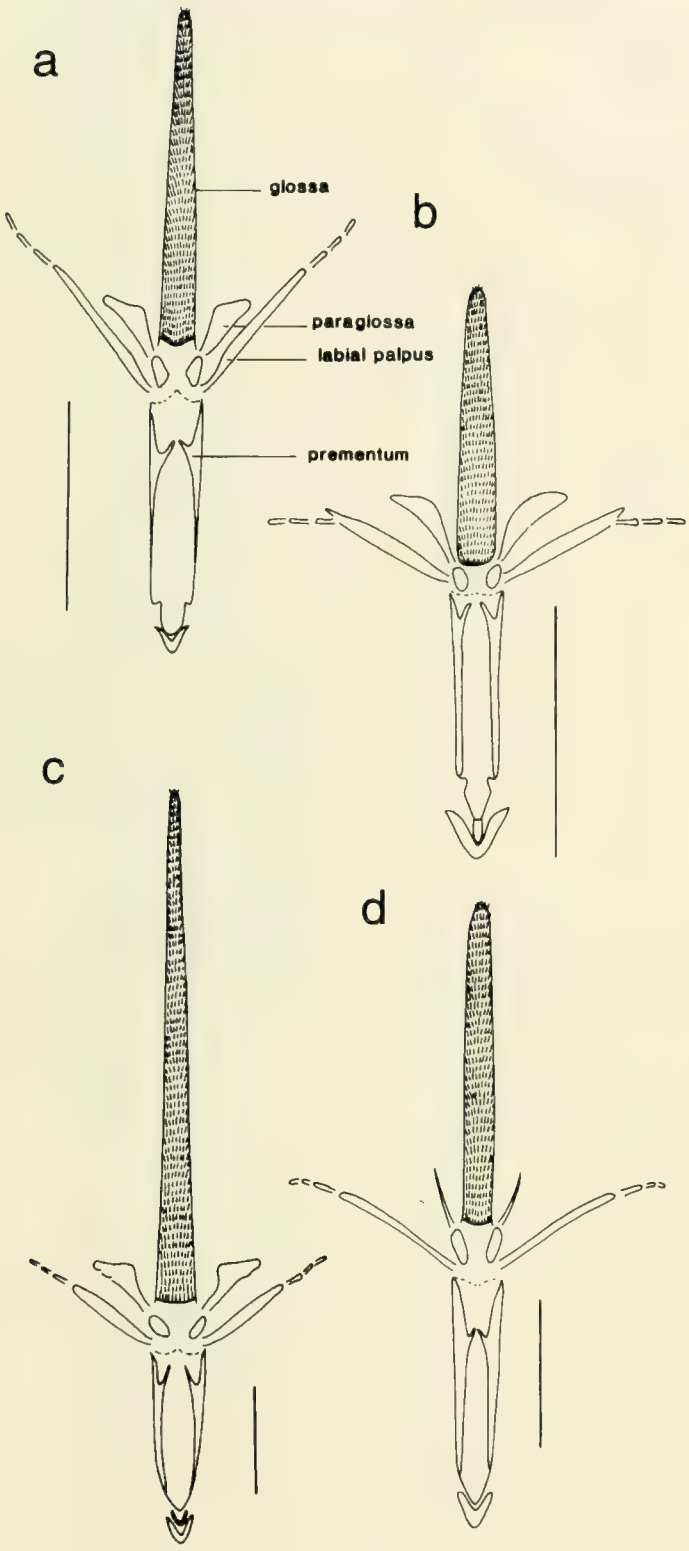


Fig. 3. Dorsal views of labia: **(a)** *P. (Cockerellula) azteca,* **(b)** *P. (Macroteropsis) echinocacti,* **(c)** *P. (Macrotera) bicolor,* **(d)** *P. (Cockerellia) albipennis.* Scale bar = 1.0 mm.

Both character states occur within *Perdita,* as well as within the outgroups studied (e.g., 1(1) in *Callonychium mandibulare* and *Pterosarus albitarsis;* 1(0) in *Calliopsis andreniformis* and *Panurginus occidentalis*). Therefore, based on outgroup morphology, it is unclear what the primitive state is for *Perdita.* However, broad paraglossae appear to be related to the application of a cell lining in species of *Perdita* studied to date. Because a cell lining is plesiomorphic for the genus, based on outgroup comparison, I assume that the broad paraglossae are also primitive for *Perdita.* Although coded 1(1) in the data matrix, *P. sphaeralceae* and *P. wootonae* (Ventralis group) show slight broadening of the paraglossae.

2(0) Female maxillary palpus with 6 segments (Fig. 4b, c); **(1)** with 5 segments (Fig. 4d); **(2)** with 3 segments (Fig. 4e).

All outgroup taxa studied have six-segmented maxillary palpi.

3(0) Acute male genal projection lacking; **(1)** acute male genal projection present (Fig. 5b), at least in some specimens.

Male genal projections are lacking in all outgroups studied and therefore 3(0) is considered plesiomorphic for *Perdita.*

4(0) Male second medial cell present (Fig. 6d); **(1)** male second medial cell lacking, i.e., veins Cu1a and 2m-cu spectral (Figs. 6c, e).

In all outgroups studied and many species of *Perdita,* the veins delimiting the male second medial cell are clearly visible in transmitted light, being well sclerotized (tubular or nebulous veins in

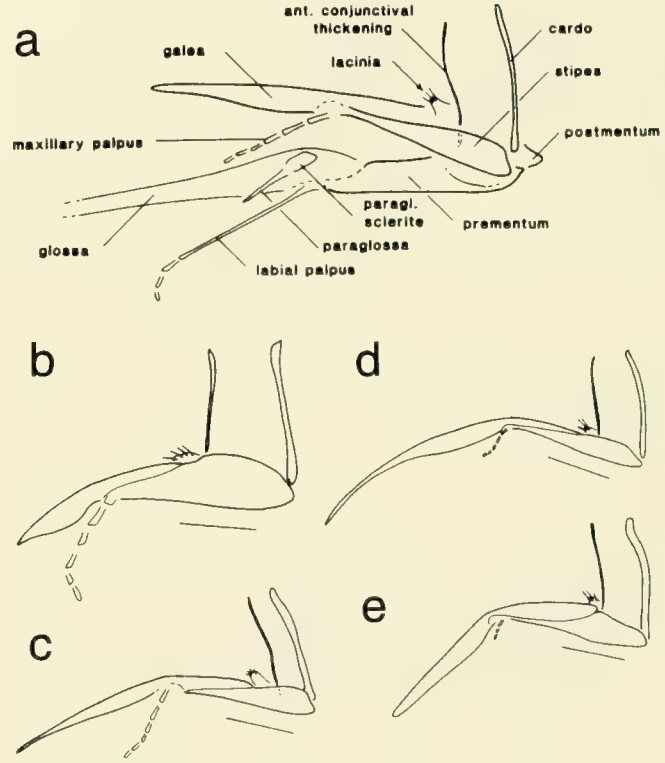


Fig. 4a. Lateral view of intact mouthparts of *Perdita texana.* **Fig. 4b-e:** Lateral views of maxillae, showing variation in the number of maxillary palpal segments: **(b)** *Panurginus occidentalis,* **(c)** *Perdita (Cockerellula) azteca,* **(d)** *P. (Procockerellia) albonotata,* **(e)** *P. (Perdita) halictoides.* Scale bar = 0.5 mm.

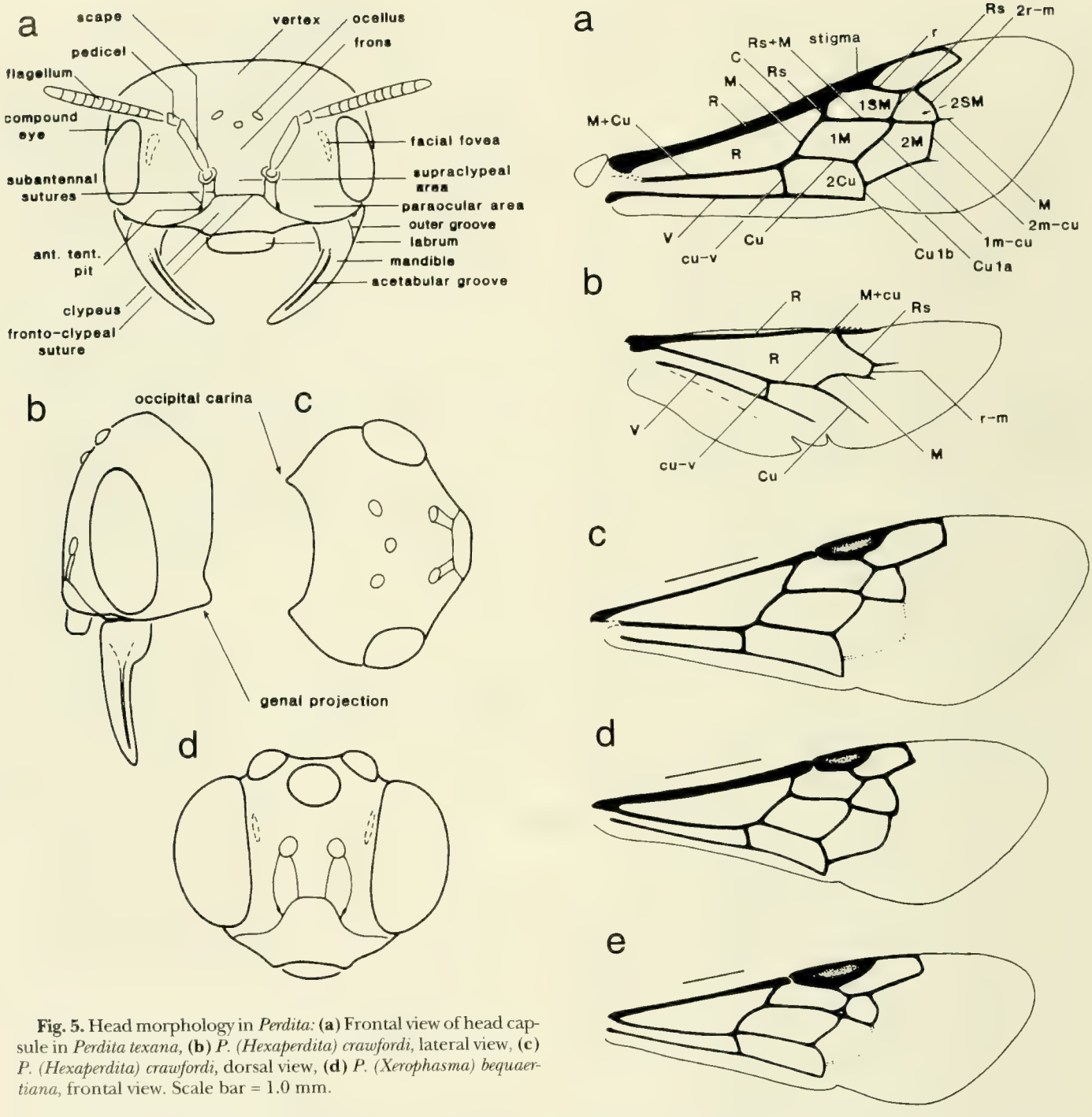


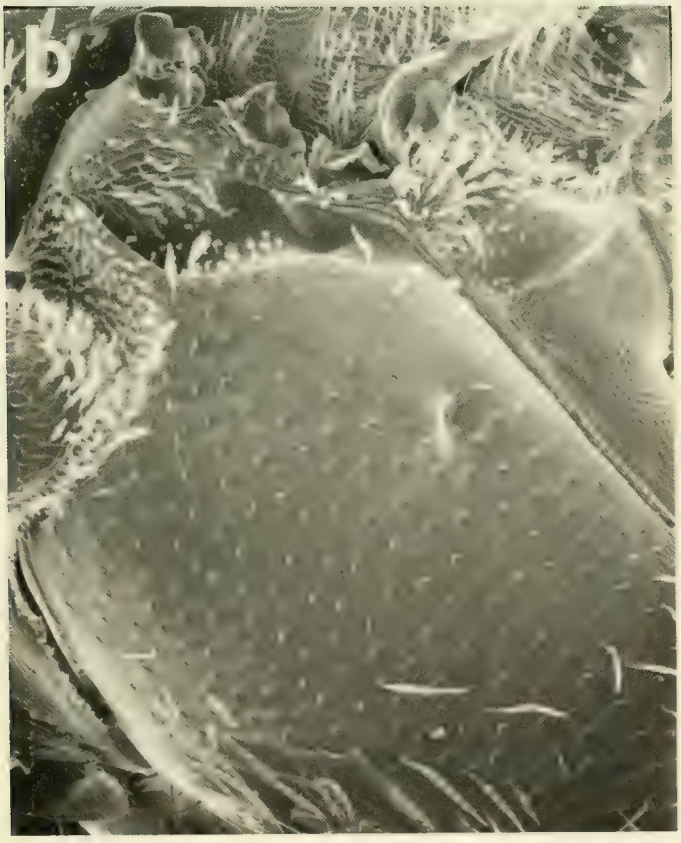
Fig. 5. Head morphology in *Perdita:* **(a)** Frontal view of head capsule in *Perdita texana,* **(b)** *P. (Hexaperdita) crawfordi,* lateral view, **(c)** *P. (Hexaperdita) crawfordi,* dorsal view, **(d)** *P. (Xerophasma) bequaertiana,* frontal view. Scale bar = 1.0 mm.

Fig. 6. Male forewings: **(a)** *P. texana* forewing with veins and cells labelled, **(b)** *P. texana* hindwing with veins and cells labelled, **(c)** *Perdita (Cockerellia) albipennis,* forewing, **(d)** *P. (Pygoperdita) californica,* forewing, **(e)** *P. (Xerophasma) bequaertiana,* forewing. Scale bar = 1.0 mm.

the terminology of Mason, 1986). In some species of *Perdita,* however, veins Cu1a and 2m-cu are invisible in transmitted light (spectral, in Mason's terminology) and therefore the second medial cell is lacking. All female *Perdita* possess a complete second medial cell.

5(0) Pre-episternal groove absent or present but not extending to scrobe (Figs. 7b); **(1)** Pre-episternal groove plus scrobal groove together forming C-shaped sulcus extending from upper edge of mesepisternum (below the forewing articulation) to scrobe (Fig. 7a).

Primitively, bees appear to possess two grooves on the mesepisternum. For example, in most Colletidae and Halictidae (excluding Nomiinae) there is a conspicuous pre-episternal groove extending downward from the upper margin of the mesepister-



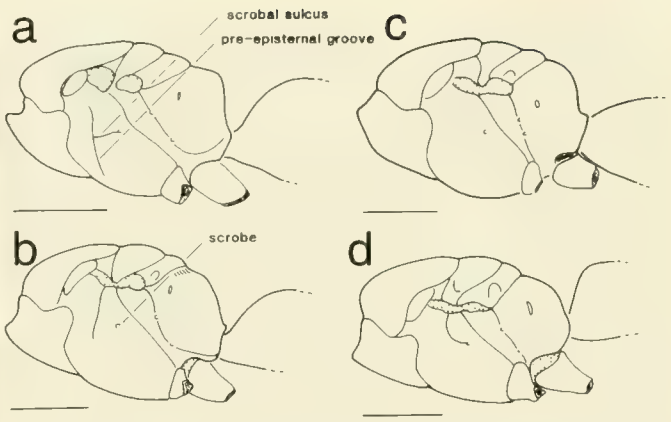


Fig. 8. Lateral views of thoraces. **(a)** *Lasioglossum zephyrum* (Halictidae), **(b)** *Pterosarus albitarsus*, **(c)** *Perdita texana*, **(d)** *Perdita albipennis*. Scale bar = 1.0 mm.

num, immediately below the forewing base (Fig. 8a). In most Colletidae this groove is very long and can reach the underside of the mesepisternum. Extending posteriorly from the pre-episternal groove and usually ending at the scrobe is the scrobal groove (Michener, 1944). Most outgroups possess only the extreme upper portion of the episternal groove and no trace of the scrobal groove (e.g., *Arhysosage flava*, *Pterosarus albitarsus*, Fig. 8b), while some others show no sign of either groove (e.g., some *Calliopsis*). In *Perdita* some species, like the outgroups, show no sign of a scrobal or pre-episternal groove (Fig. 8c). In the vast majority of *Perdita* species, however, there is a discrete groove extending from the upper margin of the episternum to the scrobe (e.g, *Perdita albipennis*, Fig. 8d). This groove appears to consist of both a pre-episternal groove (dorsally) and a scrobal groove (immediately anterior to the scrobe). Ruz referred to the entire groove as simply the pre-episternal groove. Because this state was not seen in any panurgine outgroups (except *Acamptopoeum*) it is considered derived for *Perdita*, in spite of the fact that similar grooves extending to the scrobe are present in many, more distantly related bees (e.g., some Apidae).

6(0) Male S7 with posterior margin straight or with weak emargination (Fig. 9a,b); **(1)** posterior margin moderately emarginate (depth of emargination equal to length of sclerite at midline) (Fig. 9c,d); **(2)** posterior margin deeply emarginate such that depth of emargination much greater than length of sclerite at midline (Fig. 9e,f); **(3)** emargination of S7 extreme, such that S7 appearing as two lateral, quadrate plates connected by thin bar of cuticle (Fig. 9g,h).

Some outgroups studied (those species in the Calliopsini and Melitturgini) have the male S7 highly modified in comparison to the anterior sterna and in comparison to those of *Perdita*, and therefore provide little information on character polarity within *Perdita*. Species in the Anthemurgini and Panurgini, however, have state 6(0), and this character state is considered plesiomorphic for *Perdita*.

7(0) Male S8 elongate and slender except for apodemal arms and with anterior end at most slightly expanded laterally (Fig. 9a,c,d,e); **(1)** apex expanded laterally and obtuse, and anterior end of disc expanded laterally or forked (Figs. 133-139, 141-153; Timberlake, 1954) (Fig. 9b); **(2)** disc of S8 expanded laterally and deeply forked anteriorly (Figs. 154-172; Timberlake, 1954) (Fig. 9f-h).

Fig. 7. Lateral views of thoraces [SEM]. **(a)** *P. (Macroteropsis) portalis* [scrobal groove present], **(b)** *P. (Perdita) octomaculata* [no groove].

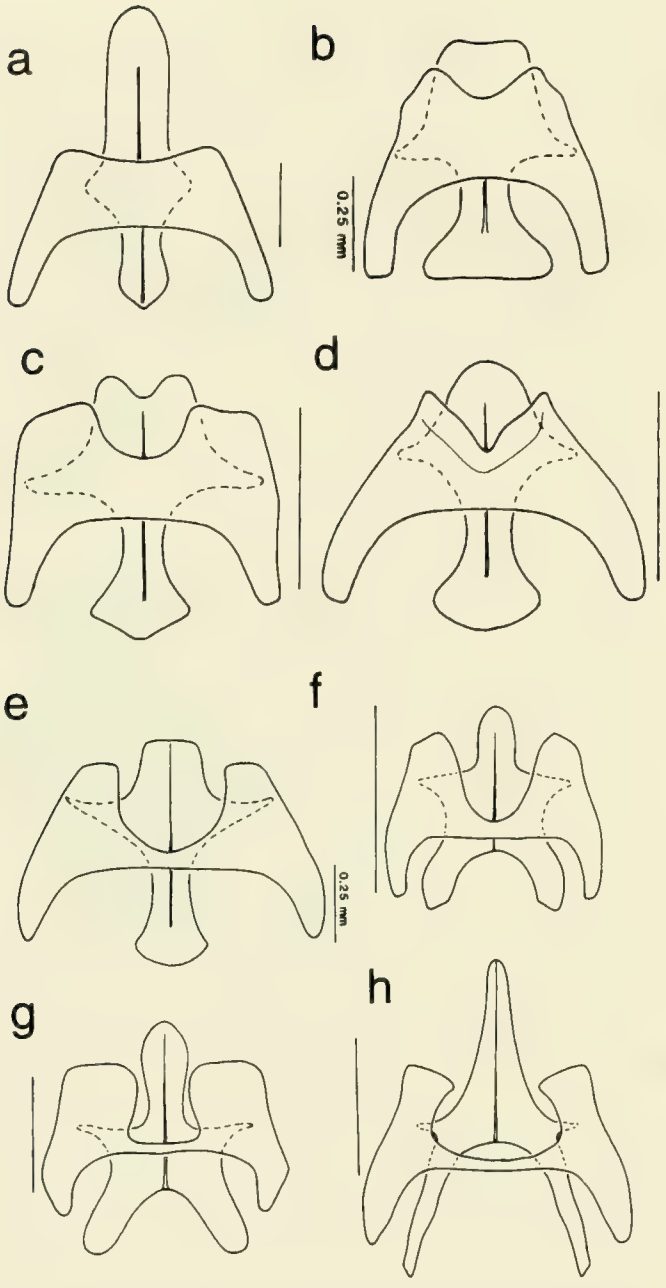


Fig. 9. Male S7 and S8, ventral views. **(a)** *Perdita (Macrotera) texana,* **(b)** *P. (Epimacrotera) euphorbiae,* **(c)** *P. (Perdita) sphaeralceae,* **(d)** *P. (Perdita) octomaculata,* **(e)** *P. (Perdita) zonalis,* **(f)** *P. (Hexaperdita) bishoppi,* **(g)** *P. (Cockerellia) coreopsidis,* **(h)** *P. (Procockerellia) albonotata.* Scale bar = 0.5 mm, except where indicated.

The male S8 can be divided into a region anterior to the apodemes (disc) and a region posterior to the apodemes (apex), which is usually exposed at the apex of the male metasoma. Because the near outgroups of *Perdita* (Calliopsini and Melitturgini) have the male S8 unlike those seen in *Perdita,* I used the Panurgini and Andreninae to polarize this character.

8(0) Antecosta of female S6 unmodified (Fig. 10c,d); **(1)** antecosta

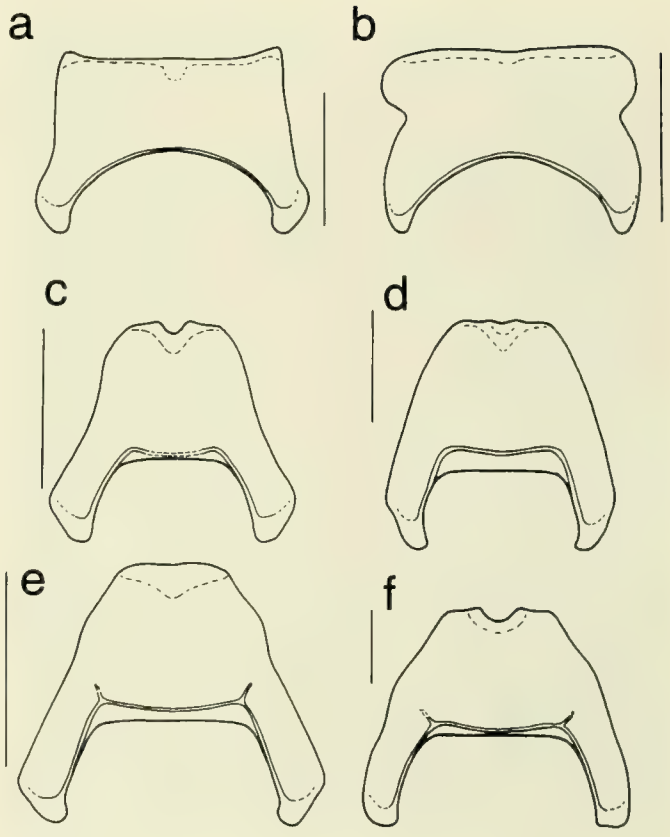


Fig. 10. Female S5 and S6. S5: **(a)** *P. (Macrotera) texana,* **(b)** *P. hurdi* (Scale bar = 1.0 mm). S6: **(c)** *Perdita (Alloperdita) mitchelli,* **(d)** *P. (Xerophasma) bequaertiana,* **(e)** *P. (Hexaperdita) bishoppi,* **(f),** *P. (Callomacrotera) maritima* (Scale bar = 0.5 mm).

of female S6 with faint, sclerotized ridge on internal surface extending posteriad from bend of antecosta (Fig. 10e,f).

Character state 8(1) can only be seen in disarticulated sixth sterna under transmitted light. The paired ridges are visible as faint lines extending posterolaterally from the angles on the antecosta at the junction of the apodemal arm and the disc of the sternum. This faint ridge is absent in all outgroups studied.

9(0) Lateral margin of female S5 straight (Fig. 10a); **(1)** lateral margin of S5 with small emargination (Fig. 10b).

The emargination is lacking in all outgroups studied and in some *Perdita.* Therefore, 9(0) is considered plesiomorphic for *Perdita.*

10(0) Outer groove of mandible as in most bees, a narrow groove apically but basally broadening to form the outer interspace (Fig. 11a) (terminology based on Michener & Fraser, 1978); **(1)** outer groove of mandible remaining discrete basally and extending diagonally across mandible to acetabulum, forming discrete outer mandibular sulcus in both sexes (Fig. 11b).

The discrete outer mandibular sulcus is absent in all outgroups studied. This character is apparently related to the dispersal of mandibular gland product because the mandibular gland opens at the base of this sulcus, near the mandibular acetabulum.

11(0) Lateral surfaces of male pronotum unmodified (Figs. 12a, 13a); **(1)** internal lateral surface of male pronotum with paired

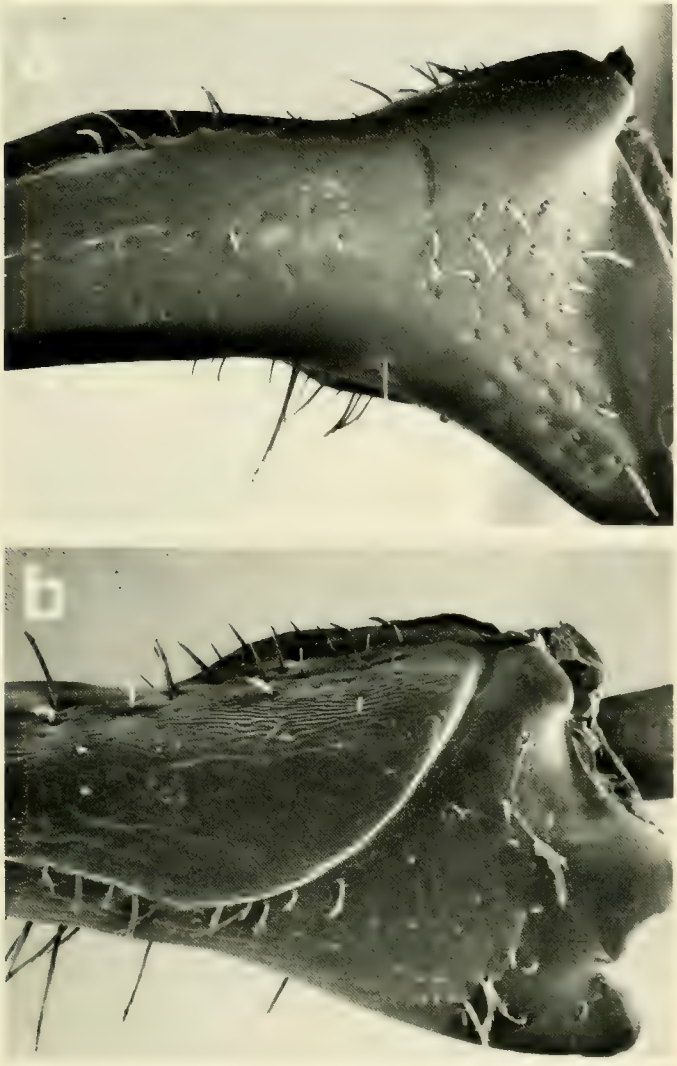


Fig. 11. Mandibles, lateral view [SEM]: **(a)** *P. octomaculata* (male) [showing lack of sulcus], **(b)** *P. texana* (male) [showing sulcus present].

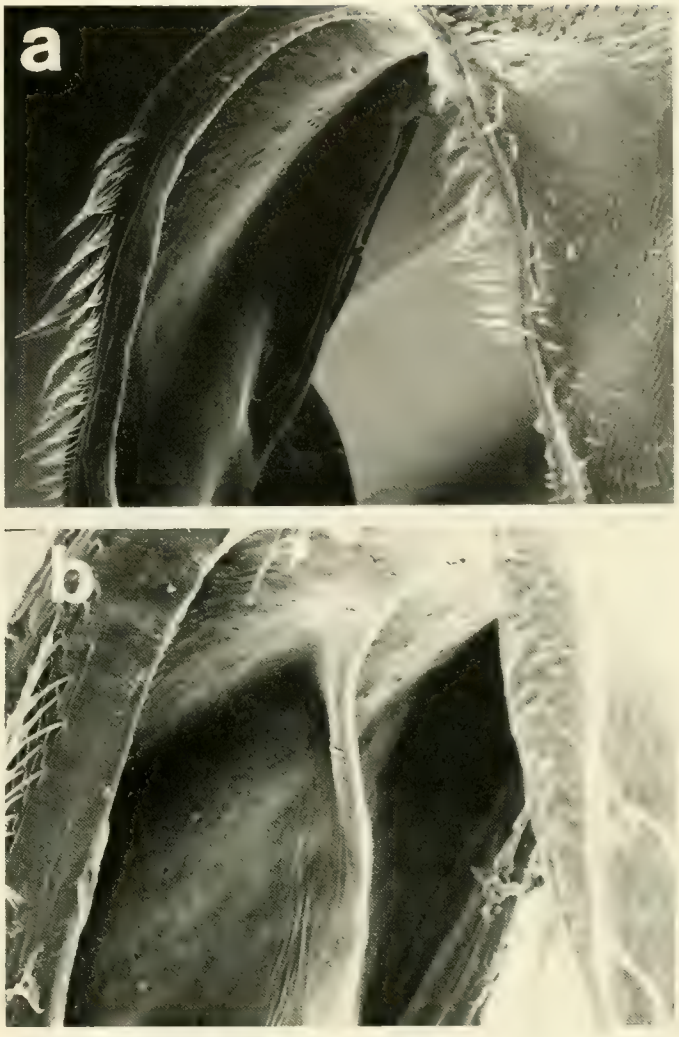


Fig. 12. Internal surfaces of male pronota [SEM] **(a)** *P. (Macrotera) texana* [pronotal carina absent], **(b)** *P. (Pygoperdita) interrupta* [pronotal carina present].

dorso-lateral carinae (Fig. 12b); **(2)** lateral surface of male pronotum with deep groove visible externally (carina may be continuous dorsally with groove) (Figs. 13b,c).

Like the corresponding female pronotal character (character 21), this character is best seen in cleared specimens. The character states are similar to those of character 21, but because the taxonomic distribution of the two characters differs they are not redundant. For example, although the presence of a deep groove in female pronota is found in only one subgenus (*Callomacrotera*), deeply grooved male pronota are found in at least four subgenera. All outgroups studied had 11(0).

12(0) Scopal hairs arising from flattened outer surface of tibia simple; **(1)** branched; **(2)** finely crinkled and unbranched.

In many species the hairs on the outer edges of the tibia are minutely branched but this character relates only to the setae on the flattened central portion. All outgroups examined had simple scopal hairs. Finely crinkled scopal hairs occur in some species within *Pterosarus* and *Pseudopanurgus*, and appear in these genera, as in *Perdita*, to be associated with carrying pollen of Asteraceae (J. Neff, pers. comm.).

13(0) Male hind basitibial plate present and well defined; **(1)** weak (rim, though complete, weakly distinguished from surrounding area); **(2)** absent (rim delineating plate incomplete).

All outgroups possess well-developed basitibial plates.

14(0) Female hind basitibial plate present and well defined; **(1)** absent.

15(0) Male tarsal claw pattern 2-2-2; **(1)** 2-2-1.

A "2" indicates a bifid claw and "1" indicates a simple claw. All outgroups have bifid tarsal claws, both in males and females (Character 16).

16(0) Female tarsal claw pattern 2-2-2; **(1)** 2-1-1; **(2)** 1-1-1.

17(0) Upper margin of male mandible lacking medial dilation; **(1)** upper margin with single acute projection originating at base (as

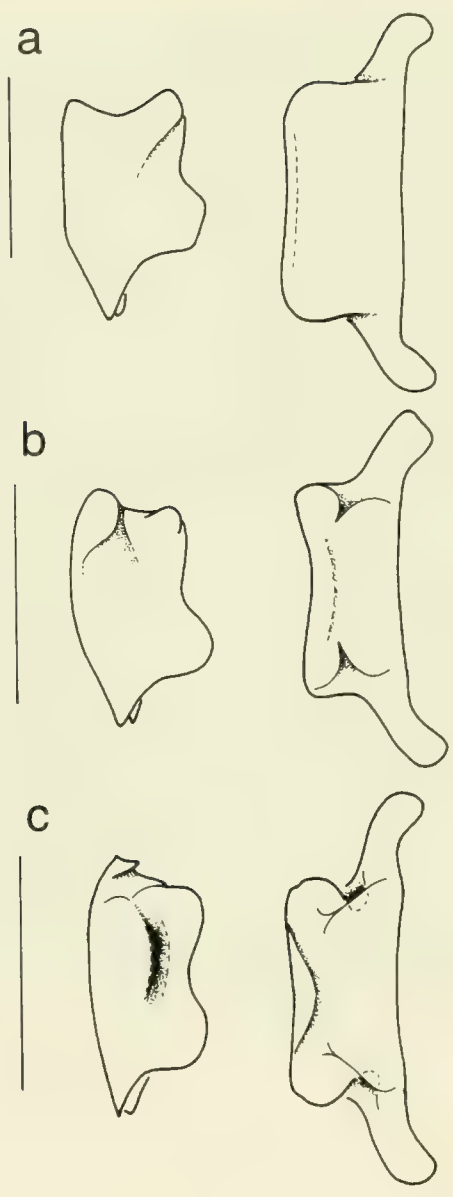


Fig. 13. Male pronota, lateral and dorsal views: **(a)** *P. (Macrotera) texana*, **(b)** *P. (Procockerellia) albonotata*, **(c)** *P. (Cockerellia) coreopsidis*. Anterior is to the left. Scale bar = 1.0 mm.

in *Callomacrotera*); **(2)** upper surface with paired acute projections arising at about midpoint along length (as in *P. turgiceps*).

18(0) Upper margin of female mandible lacking medial dilation; **(1)** upper margin dilated obtusely; **(2)** upper margin dilated acutely.

19(0) Female mandible gradually curving to apex; **(1)** female mandible abruptly angled beyond middle (angle > 45 degrees).

20(0) Apical margin of male T7 lacking ventral processes; **(1)** apical margin with median, longitudinal lamellate keel projecting ventrally or with two submedial, longitudinal lamellae projecting ventrally.

In most species of *Perdita*, and all outgroups studied, the male T7 differs from the previous terga in that the lateral edges are wrapped more ventrally, giving it a more tubular shape. There is a very weakly defined pygidial plate in some species, and there are usually stout, finely branched setae apically. In constrast, species in the subgenus *Pygoperdita* possess conspicuous single or paired ventrally-directed lamellae along the distal margin. Timberlake (1956:275) distinguished two groups within the subgenus *Pygoperdita* (Californica and Interrupta groups) based on this character, but the distinction between the two groups is weak. Based on outgroup comparison, 20(0) is plesiomorphic for *Perdita*. (See Timberlake, 1956:337-367 for illustrations of male T7 in *Pygoperdita*.)

21(0) Female pronotum lacking internal dorso-lateral carinae and grooves; **(1)** acute, lamellate internal dorso-lateral carinae present; **(2)** deep, dorso-lateral impression present.

In cleared pronota of *P. laticauda* one can see distinct internal carinae continuous dorsally with the dorsal internal carina. The lateral carinae end at about 1/4 to 1/3 the height of the pronotum in lateral view (21[1]). In some species (*P. maritima*) the internal carina is lacking, but at roughly the same position one sees a deep inpocketing of the cuticle to form an interior projection (21[2]). The similarity in the positions of the deep impression and of the lateral carina lead me to believe they are homologous. Finally, in other species there is no indication of a carina or deep impression (e.g., *P. texana;* 21[0]). At first glance *P. turgiceps* apparently lacks the internal carina; however, on close inspection one can see a minute carina. All outgroups studied possess 21(0).

22(0) Antero-dorsal rim of male pronotum unmodified (Fig. 13a); **(1)** antero-dorsal rim of male pronotum with small transverse projection or collar (Fig. 13b,c).

In lateral view, the male pronotum of some species (e.g., *P. mitchelli, P. maritima, P. zonalis*) has a prominent dorsal projection or bump at the leading edge of the pronotum (just behind the head). This projection is formed as a result of a deep transverse sulcus passing very near the anterior rim of the pronotum. When the transverse sulcus passes across the pronotum roughly at the midpoint of the pronotum, no prominent projection is formed anterior to the sulcus. The trait is especially pronounced in males, but a similar character is found in female pronota. All outgroups studied lack the projection.

23(0) Antero-medial angle of the prosternal apophysis in females prominent, acute and located more dorsally; **(1)** inconspicuous, obtuse and located more ventrally.

In lateral view of the female prosternum, one sees two sets of paired processes projecting anteriorly from the dorsal, anterior corner of the sternal apophysis. The postero-dorsal angle of each propleuron articulates with the prosternum at a broad, depressed area, set off from the rest of the prosternal apophysis by a low carina, between these two processes. Michener (1944) called these processes the antero-medial angle of the apophyseal arm (the more ventral process) and the antero-dorsal angle of the apophyseal arm. In most species of *Perdita* (e.g., *P. lacteipennis* and *P. halictoides*), the antero-medial angle is prominent, acutely pointed and located close to the antero-dorsal angle. However, in the subgenus *Pseudomacrotera* the antero-medial angle is much less prominent, obtuse and is located more ventrally, as in some outgroups (e.g., *Acamptopoeum prinii* and *Meliturga clavicornis*). Both states of this character are present in the outgroups so it is impossible to polarize this character.

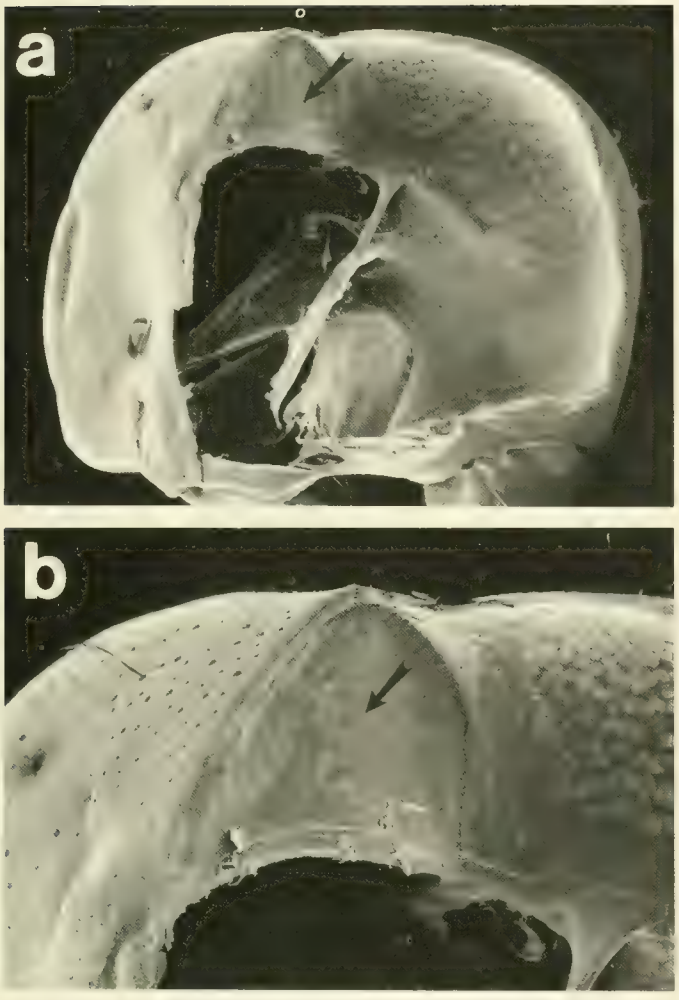


Fig. 14. Internal anatomy of male head capsule in *P. texana* [SEM]: **(a)** oblique view of head capsule showing median cephalic lamella (indicated by arrow), **(b)** close-up of median cephalic lamella (indicated by arrow), showing sites of muscle attachment.

24(0) Median internal cephalic lamella absent; **(1)** lamella present along midline of head capsule (Figs. 14a, b).

A median internal cephalic lamella, extending from the anterior ocellus nearly to the occipital foramen, is present in both males and females of all species of *Perdita* studied, and is lacking in all outgroups. The presence of this lamella is considered a synapomorphy of *Perdita*. The median cephalic lamella serves as a site of attachment for the mandibular adductors.

25(0) In females, tentorial bridge separated from roof of proboscidial fossa; **(1)** tentorial bridge broadly fused to roof of proboscidial fossa.

In some species (e.g., *P. texana, P. lacteipennis* and *P. californica*) the bridge of the tentorium lies distinctly above the roof of the proboscidial fossa and the two are connected by a thin vertical lamella of cuticle. In ventral view, the roof of the proboscidial fossa, has a dark line running along its midline which corresponds to the internal vertical lamella. In other species (e.g., *P. zonalis, P. bequaertiana*) the tentorial bridge is fused broadly to the inner surface of the roof of the proboscidial fossa and no lamella is visible in lateral view. All outgroups studied, except *Acamptopoeum prinii*, have the tentorial bridge dorsal to the proboscidial roof, with the two separated by a thin lamella (25[0]).

26(0) Occipital region in male unmodified; **(1)** occipital region with paired arcuate carinae on either side of occipital foramen (preoccipital carinae) (Fig. 5c).

In dorsal view of the occipital region of the head one sees two sharp carinae on either side of the occipital foramen in the males of some species (e.g., *P.* (*Hexaperdita*) *bishoppi*). Most species of *Perdita* and all outgroups studied lack such carinae.

27(0) Second submarginal cell lacking (two submarginal cells; Fig. 6c, d); **(1)** small, triangular, intercalary second submarginal cell present (three submarginal cells; Fig. 6e).

In five species of the subgenus *Alloperdita* and in all species of *Xerophasma*, a small second submarginal cell is present. In all other species of *Perdita* there are only two submarginal cells. Based on their shape and position, it is likely that the two submarginal cells present in most species of *Perdita* are homologous to the first and third submarginal cells in those species possessing three submarginal cells. Because all outgroups, except *Melitturga clavicornis*, lack the second submarginal cell, it is most likely a derived state within *Perdita*. Timberlake (1956:271-273), however, considered the possession of three submarginal cells primitive for *Perdita*. For bees as a whole three submarginal cells is certainly plesiomorphic, but the second submarginal cell of many bees and the small triangular cell seen in a few *Perdita* species are probably not homologous.

28(0) In females, graduli present, in some form, on S2-S5 (Fig. 15a); **(1)** graduli entirely lacking on S2-S5 (Fig. 15b).

All species of *Perdita* studied lack graduli on S2-S5. Because all panurgine outgroups studied have either medial, paired lateral, or complete (continuous medial and lateral portions) graduli, the lack of sternal graduli is considered a synapomorphy of *Perdita*.

29(0) Broad pale membranous line on antero-lateral corner of female T5 absent or present but not reaching the spiracle (Fig. 16a); **(1)** slender pale membranous line reaching, or nearly reaching, spiracle (Fig. 16b, c).

In all species of *Perdita* the female T5 in lateral view has narrow transparent membranous lines extending from the antero-lateral corners, just beneath the apodemes, posteriorly to the spiracles. Homologous pale regions are present in other terga but are most easily seen in T5. These pale regions are membranous and allow the lateral portions of the terga to move with respect to the dorsal part, possibly allowing dorso-ventral expansion and contraction of the metasoma. Since these membranous areas are small and do not reach the spiracle in any of the outgroup taxa studied, their presence is considered a synapomorphy of *Perdita*.

30(0) Pale membranous line on female T1 narrow and passing beneath spiracle; **(1)** line broad, enclosing spiracle; **(2)** line absent or present but not reaching spiracle.

In all outgroup taxa studied there are paired transparent membranous lines extending backwards from the antero-lateral corners of T1, passing beneath the spiracle and ending somewhat posterior of each spiracle. This state has been found in only one species of *Perdita, P. turgiceps*, and is considered primitive for *Perdita*.

31(0) Pale membranous line on antero-lateral corners of male T6

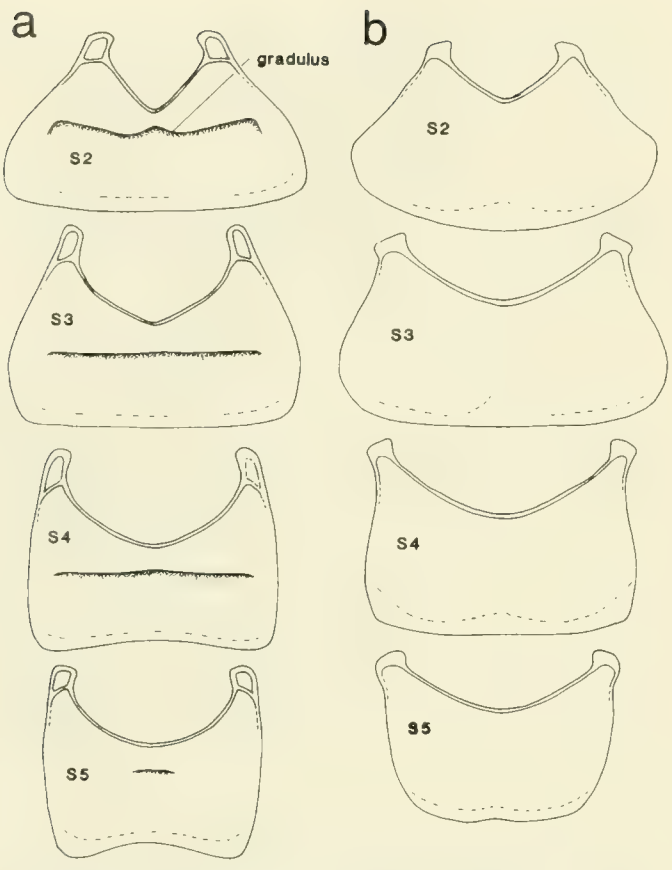


Fig. 15. Female sterna 2-5. **(a)** *Pterosarus albitarsus*, **(b)** *Perdita (Callomacrotera) maritima.*

absent (Fig. 16d, e); **(1)** pale membranous line reaching, or nearly reaching, spiracle (Fig. 16f).

Because the outgroup taxa studied lack the membranous line, 31(0) is considered primitive.

32(0) Posterior margin of female S1 straight or very slightly emarginate medially (Fig. 17a) ; **(1)** margin deeply but gradually and obtusely emarginate (Fig. 17b); **(2)** margin deeply and acutely emarginate medially (Fig. 17c).

All outgroups lack a pronounced medial emargination and therefore 32(0) is considered primitive.

PHYLOGENETIC ANALYSIS

The data matrix was analyzed two ways. In the initial analysis, all of Timberlake's subgenera were included except for the monotypic *Xeromacrotera* (*P. cephalotes*), which is only known from the male. The placement of *P. cephalotes is* discussed in a second analysis, presented below. In the analyses, all characters were treated as unordered (non-additive) except for multistate characters 2, 6, 13 and 32, for which the character states could be logically connected by a linear sequence (e.g., character 2: maxillary palpi 6-segmented -> 5-segmented -> 3-segmented).

In the first analysis the m*, bb* options of Hennig86 resulted in 12 equally parsimonious trees of length 84 and con-

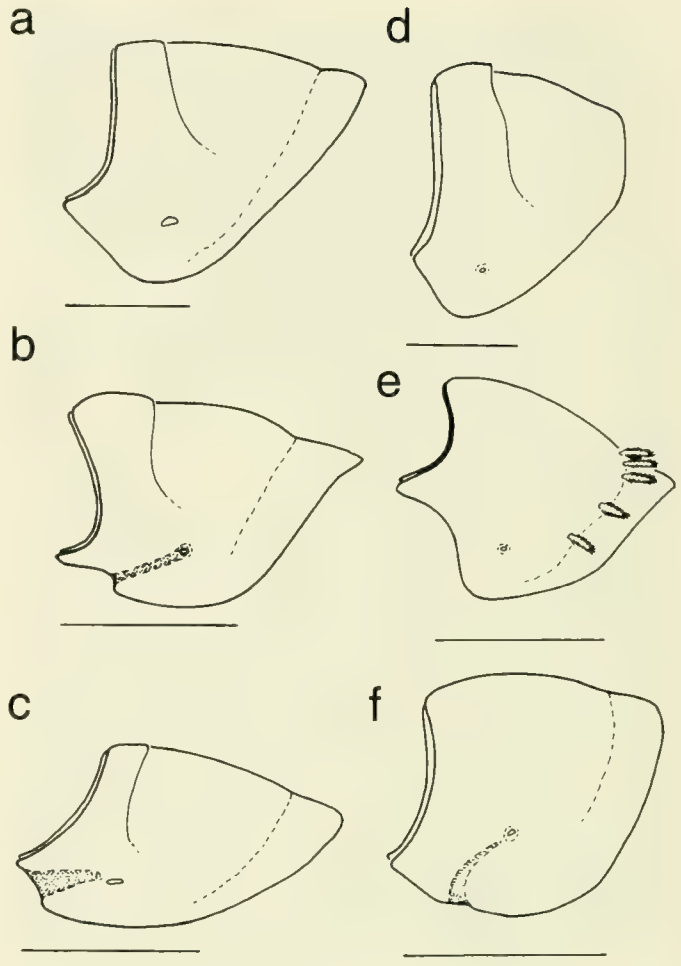


Fig. 16. Lateral views of female T5 and male T6. Female T5: **(a)** *Pterosarus albitarsus*, **(b)** *Perdita (Cockerellula) anthracina*, **(c)** *P. (Cockerellia) albipennis.* Male T6: **(d)** *Pterosarus albitarsus*, **(e)** *Perdita latior*, **(f)** *P. (Glossoperdita) pelargoides.* Scale bars = 0.5 mm.

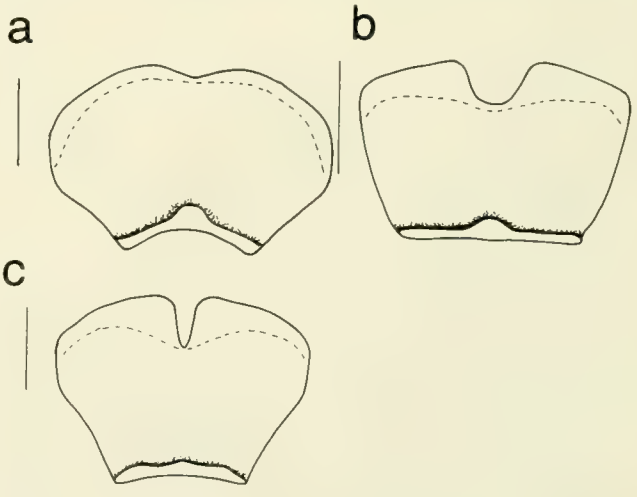


Fig. 17. Female S1. **(a)** *P. (Cockerellula) laticauda*, **(b)** *P. (Epimacrotera) euphorbiae*, **(c)** *P. (Perdita) zonalis.* Scale bar = 0.25 mm.

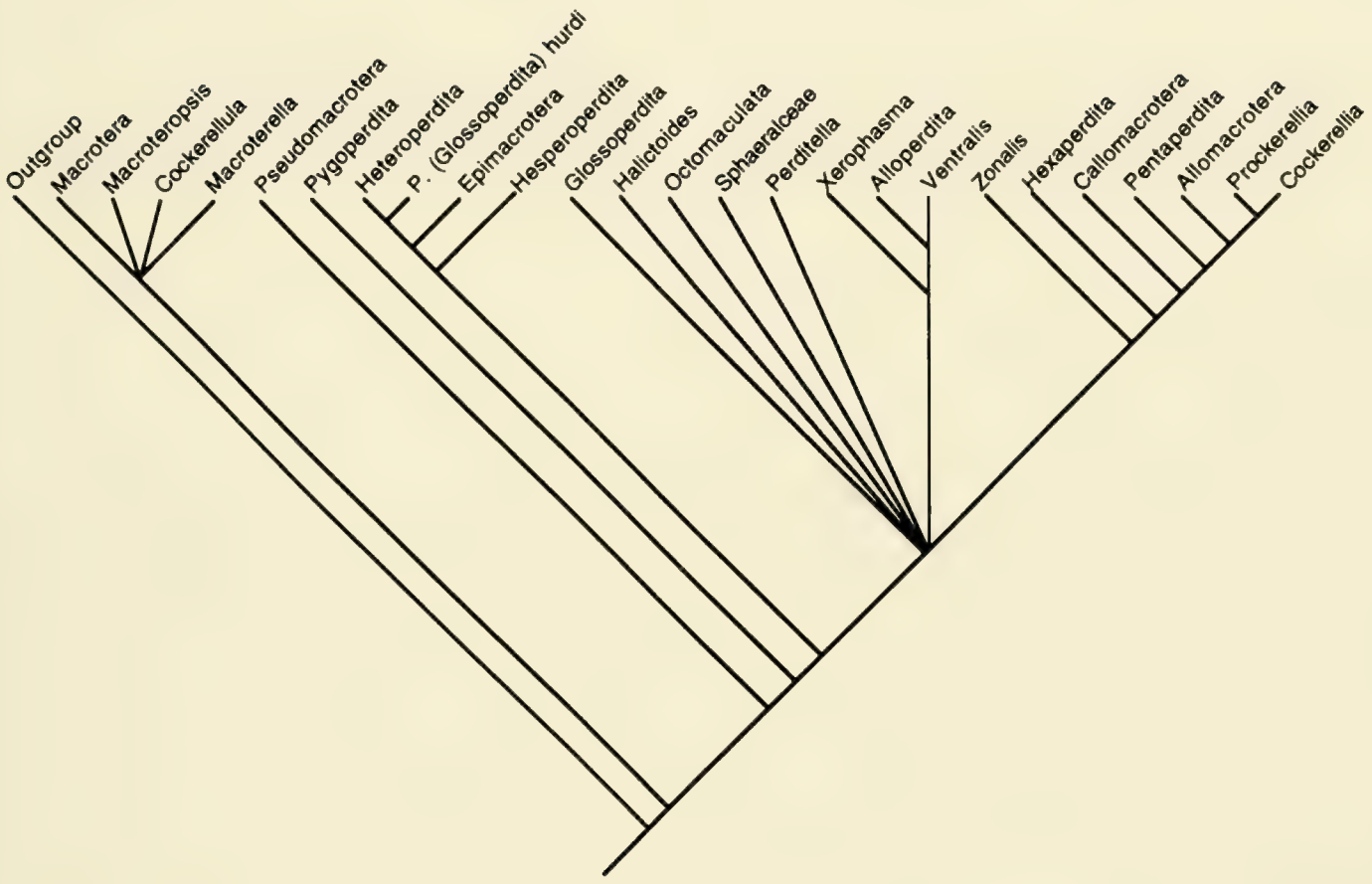


Fig. 18. Consensus tree of 6 equally parsimonious trees for subgeneric analysis. The subgenus *Perdita* includes the Halictoides, Octomaculata, Sphaeralceae, Ventralis and Zonalis groups.

sistency index of 54 for the 32 characters and 28 taxa (*Xeromacrotera* excluded). Among these 12 trees there were 6 distinct topologies. Figure 18 shows the consensus tree, Fig. 19 a-f show the 6 equally parsimonious resolutions of the single polytomy, and Fig. 20 shows the characters mapped on the preferred tree, as discussed below.

Monophyly of *Perdita*. The monophyly of the genus is supported by three unique and un-reversed characters (Fig. 20): the presence of an internal median cephalic lamella, not known to occur in any other bees (24[1]; Fig. 14); the lack of sternal graduli in females (28[1]); and (3) the presence of a pale membranous line extending to the spiracle on the lateral edges of the female S6 (29[1]).

Based on Luisa Ruz's phylogeny of the Panurginae (Ruz, 1991), the monophyly of *Perdita* is supported by three additional unique and unreversed characters: (1) the male sixth sternum is three or more times broader than long (90[1]), whereas in the remainder of the panurgines S6 is at most only slightly broader than long (Fig. 21a), (2) the marginal cell is shorter than the distance from its apex to the wing tip (46[2]) and (3) the first valvifer is elongate rather than triangular (129[1]), as it is in the other panurgines. The first of these characters is variable within *Perdita*. While some species show a very slender male S6 (Fig. 21a,c,d), others (e.g., *P. echinocacti*, Fig. 21b) have a male S6 which is only twice as broad as long. Therefore, this character cannot be considered a synapomorphy of the genus. The marginal cell character holds for all species I studied. I did not investigate the third character so I cannot reject it as a synapomorphy of *Perdita*.

Relationships among the *Perdita* Subgenera. The monophyly of the subgenera *Macrotera, Macroteropsis, Macroterella,* and *Cockerellula* (herein called the *Macrotera* group) is supported by two characters (Fig. 20). Character 10(1), the presence of a discrete sulcus on the outer surface of the mandibles of both males and females, is a unique and unreversed synapomorphy of these four subgenera. Character 30(1) also supports the *Macrotera* group but arose convergently in the Sphaeralceae group of *Perdita* sensu stricto as well. The *Macrotera* group appears to form the sister group to a monophyletic group including all the remaining subgenera (*Pseudomacrotera,* plus all the taxa to its right; Fig. 20). The species-level phylogenetic relationships of the *Macrotera* group will be presented below.

Interestingly, the placement of the *Macrotera* group at the base of the tree is consistent with the existence of ple-

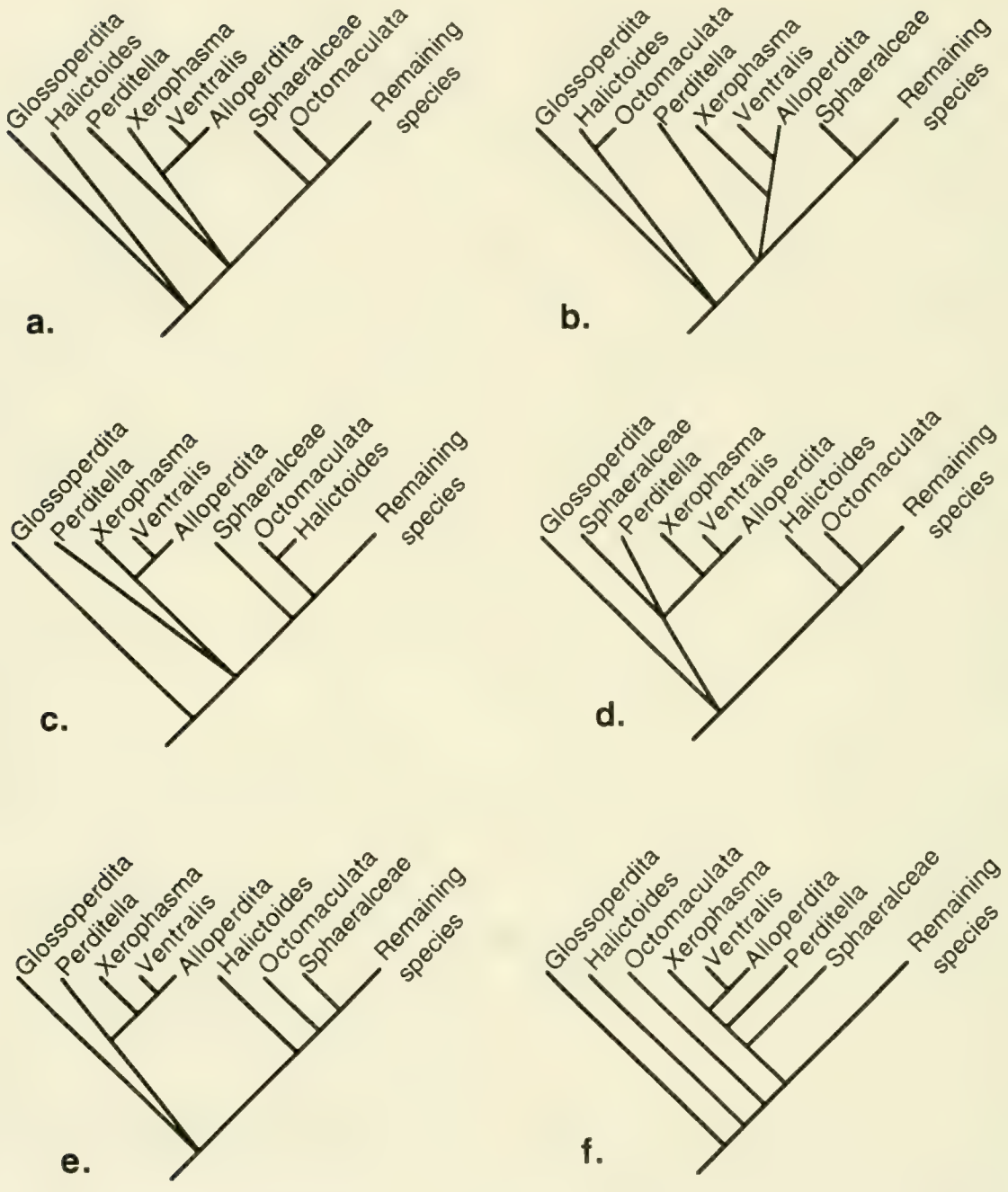


Fig. 19 a-f. Six equally parsimonious resolutions of the consensus tree shown in Fig. 18.

siomorphic behavioral characters in the species which have been studied so far. The placement of larval fecal material on the rear wall of the cell in *P.* (*Macrotera*) *texana* (Neff & Danforth, 1991), *P.* (*Macrotera*) *pipiyolin* (Rozen & Michener, pers. comm.), *P.* (*Macroteropsis*) *portalis* (Danforth, 1991a) and *P.* (*Macroterella*) *mellea* (Rozen, pers. comm.) is similar to the placement of fecal material in the non-*Perdita* Panurginae (Rozen, 1967). However, in species of the more derived *Perdita* that have been studied (e.g., the subgenera *Perdita* and *Cockerellia*), feces are placed on the venter of the larva (Rozen, 1967; Danforth, 1989b). Similarly, the presence of a hydrophobic lining on the inner surface of the cell is shared by *P. texana, P. bullocki, P.* (*Macroteropsis*) *latior* (Danforth, pers. obs.), *P. portalis* and *P. mellea,* as well as the non-*Perdita* panurgines (Rozen, 1989).

The monophyly of the group *Pseudomacrotera* plus all the groups to its right, is supported by three characters: the presence of a c-shaped pre-episternal groove extending from the forewing base to the scrobe (5[1]), the presence of internal dorso-lateral carinae in the female pronotum (21[1])

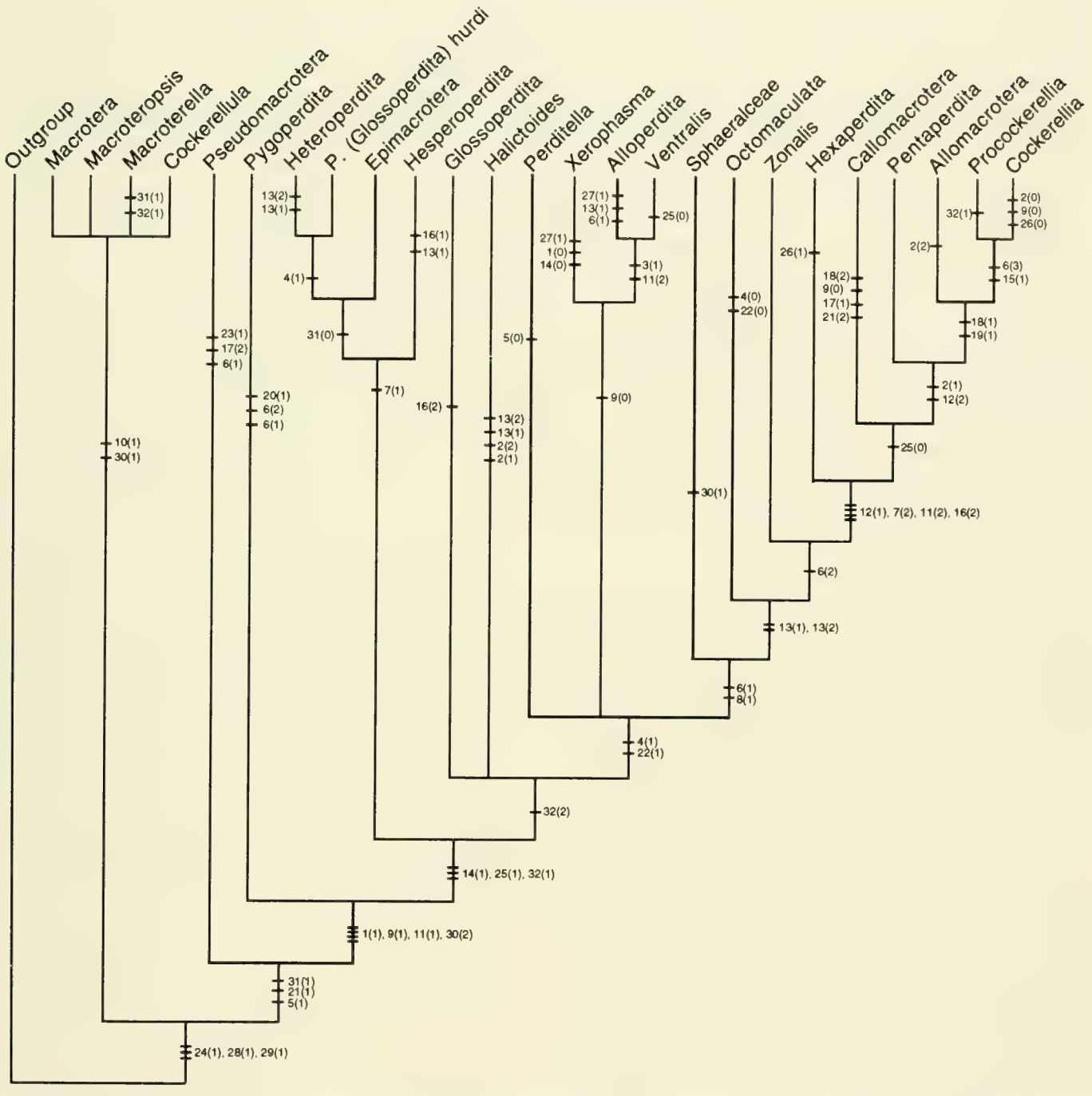


Fig. 20. Preferred tree of the six equally parsimonious resolutions of the consensus tree (Fig. 18); characters mapped onto tree.

and the presence of a pale, membranous line which reaches the spiracle on the male T6 (31[1]), although this last character is reversed in the group *Heteroperdita* + *P. hurdi* + *Epimacrotera*.

The group including the subgenus *Pygoperdita* and the subgenera to its right in Fig. 20 is also well supported by unique features. This group I refer to below as the "higher *Perdita*." Character 1(1), the possession of slender, acutely pointed female paraglossae, is present in all of the higher *Perdita*, except the subgenus *Xerophasma*. Although the outgroups were variable for this character, the derived state for *Perdita* appears to be 1(1). It is likely that the broad, brushlike paraglossae (1[0]), seen in the subgenera belonging to the *Macrotera* group, are used in the application of the hydrophobic coating to the cell wall. I have seen female *P. portalis* construct cells in observation nests and in the final

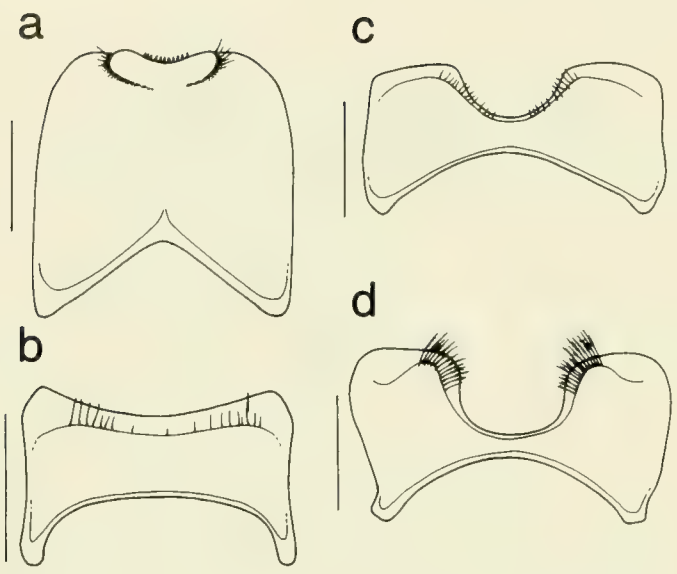


Fig. 21. Male S6, showing depth of emargination along posterior margin: **(a)** *Panurginus occidentalis,* **(b)** *Perdita (Macroteropsis) echinocacti,* **(c)** *P. (Perdita) zonalis,* **(d)** *P. (Procockerellia) albonotata.* Scale bar = 0.5 mm.

stages the walls of the cell were brushed with the paraglossae, apparently in the application of the hydrophobic cell coating (Danforth, 1991a)

Other characters which support the monophyly of the "higher Perdita" are 30(2), 9(1), the small emarginations on the lateral margins of the female S5, and 11(1), the carinae on the internal surface of the male pronotum, although the latter two characters had low consistency (ci = 25 and 50, respectively).

The subgenus *Pygoperdita* is clearly monophyletic based on the present analysis. In all species the seventh tergum in the male (character 20) has either paired, ventrally-directed lamellate lobes (in the Californica group) or a single, ventrally-directed bifid lobe (in the Interrupta group). Because these two states intergrade (making placement of some species difficult for Timberlake [1954]), and because there are no similar structures in other members of *Perdita,* these two conditions are considered homologous and synapomorphic for the subgenus *Pygoperdita.* The monophyly of this subgenus is further supported by the deeply divided male S7 (6[2]). Although a similarly divided S7 occurs elsewhere in the tree (uniting the Zonalis group and the subgenera to its right in Fig. 20), numerous characters support the hypothesis that these states have arisen independently.

The subgenera *Hesperoperdita, Epimacrotera, Heteroperdita* and one species previously placed in the subgenus *Glossoperdita, P. hurdi,* form a monophyletic group united by the uniquely shaped male S8 (7[1]). It is clear from this analysis that *P. hurdi* does not belong with members of *Glossoperdita.* The shape of the male S8 (7[1]) and the lack of the male second medial cell (4[1]) place *P. hurdi* as the sister group to *Heteroperdita.* Although this group of three subgenera plus *P. hurdi* appears to be monophyletic, the subgenera included in it are not all necessarily monophyletic.

According to Timberlake (1954:377), *Epimacrotera* is "similar and closely allied to *Glossoperdita.*" Timberlake later stated that "it is now becoming evident that *Glossoperdita* and *Epimacrotera* may intergrade more or less completely" (1960:129). I have found no synapomorphies for *Epimacrotera.* A possible synapomorphy mentioned by Timberlake (1954:377) is the presence of upturned hairs along the lower margin of the scopa, but I was unable to see such hairs. Females of *P. diversa* have a very unusual hind basitibial protuberance, which does not appear to be homologous to the basitibial plate in other species. This character may prove useful for resolving the relationships within this subgenus.

Hesperoperdita is apparently a monophyletic subgenus. *P. ruficauda* possesses an unusual tarsal claw pattern in the female, with a very small basal tooth on the mid and hind tarsal claws, making them appear simple, and a larger basal tooth on the fore-tarsal claws, giving them a bifid appearance (16[1]). According to the phylogenetic analysis, the weakly defined basitibial plate in *Hesperoperdita* (13[1]) is also a synapomorphy of the subgenus, but this character had rather low consistency (ci=20).

There is little doubt that the subgenus *Heteroperdita* is monophyletic. Synapomorphies of the group are the following: (1) postero-ventrally directed setae on either side of proboscidial fossa in females, (2) yellow maculation on male metanotum and/or propodeum, and (3) white, closely appressed hairs over the head and mesosoma.

The greatest source of ambiguity in this analysis involves the polytomy in Fig. 18 that includes the Halictoides, Octomaculata and Sphaeralceae groups, *Perditella, Glossoperdita,* the monophyletic group of *Xerophasma* + (*Alloperdita* + Ventralis group) and the monophyletic group including the Zonalis group and the subgenera to its right. The monophyly of this entire group is supported by the acutely emarginate posterior edge of the female S1 (32[2]; Fig. 17c). Figures 19a-f show the six equally parsimonious resolutions of the polytomy. I prefer the tree shown in Fig. 19a as the most likely resolution because the characters whose homologies I am most confident of (6 and 8) have the highest consistency indices in this resolution (ci = 42 and 100, respectively). Intuitively, I believe that the Sphaeralceae and Octomaculata groups are closely related to the monophyletic group of Zonalis and the groups to its left. The fact that there are several resolutions of this polytomy indicates real uncertainty about the relationships among these groups, and a need for more characters at these nodes.

Based on the characters included in this study, *Glossoperdita* is clearly polyphyletic, with at least one species, *P. hurdi,* belonging elsewhere, as discussed above. Timberlake originally considered this group distinct because of the elongate glossae; many species visit flowers in the Polemoniaceae. As mentioned above, he later conceded (1960:129) that the distinction between *Glossoperdita* and *Epimacrotera,* based primarily on glossa length, was weak. *P. hurdi* differs from other members of *Glossoperdita* studied in lacking a second medial cell in the male, in lacking a pollex on the male mandible and in having a short galeal comb (*P.*[*G.*] *pelargoides* lacks

a galeal comb). *P. hurdi* is larger than other members of *Glossoperdita*. Synapomorphies of *Glossoperdita*, excluding *P. hurdi*, are a distinctive pattern of metasomal maculation in males (a central yellow bar and two lateral yellow spots along the posterior margin of each tergum) and a rectangular head longer than wide.

The Halictoides group of *Perdita* sensu stricto is united by the greatly reduced maxillary palpi (2[2]), and, in this analysis, by the reduced male basitibial plates (13[2]).

The subgenus *Xerophasma*, which contains two highly apomorphic, nocturnal species, is clearly monophyletic. Both species are very large, entirely pale and have enlarged compound eyes and ocelli (Fig. 5d).

Alloperdita is united by three characters; however, none provides very convincing evidence that this subgenus is monophyletic. Characters 6(1) and 13(1) have arisen elsewhere in the tree. Character 27(1), the presence of a small, triangular, intercalary submargical cell (Fig. 6e), may have arisen independently in *Alloperdita* and *Xerophasma* (Fig. 20) or, equally parsimoniously, may have arisen once in the common ancestor of *Xerophasma, Alloperdita* and the Ventralis group, and then reversed to the plesiomorphic state in the Ventralis group. This character is variable within some species and even in some individuals, with one wing showing three submarginal cells and the other just two. The elongate, stout antennae of males is the strongest synapomorphy of *Alloperdita*.

Alloperdita and the Ventralis group are united by two characters: 3(1), the presence of male genal projections and 11(2), deep, acute grooves in the lateral surfaces of the male pronota. The latter character is also found in the monophyletic group including *Hexaperdita* plus all the groups to its right.

The subgenus *Perditella* is apparently polyphyletic. At least two species (*P. larreae* and *P. cladothricis*) possess characters which are shared by members of the *Cockerellia* group: deep impressions in the lateral surfaces of the male pronotum and male occipital carinae. The characters used by Cockerell and Timberlake to recognize this group were small size, enlarged stigma, small, triangular second submarginal cell and shortened marginal cell (Timberlake, 1956:267). All the wing venational characters are highly correlated with body size and therefore may be poor indicators of phylogenetic relationship (Danforth, 1989a). For the purposes of this preliminary phylogenetic analysis, I used *P. minima* as a representative species.

The monophyletic group of the Zonalis group plus the 6 subgenera to its right in Fig. 20 is supported by the deeply emarginate male S7 (6[2]). The group of subgenera including *Hexaperdita, Callomacrotera, Pentaperdita, Allomacrotera, Procockerellia* and *Cockerellia* clearly form a monophyletic group which I will refer to below as the *Cockerellia* group. Characters supporting this group include male S7 morphology (7[2]), male pronotal morphology (11[2]), scopal hair structure (12[1]) and the female tarsal claw pattern (16[2]). The relationships among the members of the *Cockerellia* group are well supported; the characters in this portion of the tree have high consistency and in all previous analyses of these data, this group showed virtually the same pattern of relationships.

The hypothetical transformation series shown in Fig. 20 for character 2 deserves some explanation. According to the present analysis, reduction in the number of maxillary palpal segments is considered a synapomorphy of the group including *Pentaperdita, Allomacrotera, Procockerellia* and *Cockerellia*, with a reversal to the 6-segmented condition in *Cockerellia*. Although such a reversal seems unlikely, the alternative hypothesis, that reduced maxillary palpi is a synapomorphy of *Pentaperdita, Procockerellia* and *Allomacrotera*, is incongruent with characters 6(3) and 15(1), which unite *Procockerellia* and *Cockerellia*. Analysis of the data matrix with character 2 treated as unordered resulted in the same pattern of relationships.

While the *Cockerellia* group of subgenera is clearly a monophyletic group, the subgenera which make up this group are not necessarily themselves monophyletic. For example, no unique and unreversed characters were found to support the monophyly of the subgenus *Hexaperdita*. *Hexaperdita* is united by the possession of an occipital carina in males (26[1]; Fig. 5c), although this character has arisen in *Cockerellia* as well. A character of many, though not all, species of *Hexaperdita* is the possession of a carina at the posterior margin of the male mandible, near the base. This carina was not seen in members of any other subgenera or outgroups.

One species, *P. cara*, lacked both preoccipital carinae and deep grooves in the lateral surfaces of the male pronotum. *P. cara* is also very small in comparison to other species of *Hexaperdita*. Placement of *P. cara* remains unclear, but it most likely belongs elsewhere in the genus.

The subgenus *Callomacrotera*, containing only two described species, is clearly monophyletic. Synapomorphies include the acute basal tooth on the inner surface of the female mandible, the large, robust body form, and the depressions on the dorso-lateral corners of the female pronotum (21[2]). Both species also have a highly modified male clypeus. In *P. maritima* the male clypeus is densely clothed with erect setae. In *P. acapulcona* the male clypeus is depressed and with an apical fringe of long setae overhanging the labrum.

Timberlake referred to the reduced number of maxillary palpi and the bifid metatarsal claws as features uniting *Pentaperdita* (Timberlake, 1954:404). In the present analysis the tarsal claw character is considered plesiomorphic (15[0]), and reduction in the number of maxillary palpal segments is considered a synapomorphy of the group including *Pentaperdita, Allomacrotera, Procockerellia* and *Cockerellia*, with a reversal to the 6-segmented condition in *Cockerellia*. I was unable to find any convincing synapomorphies of *Pentaperdita*.

Although the members of *Cockerellia* are a seemingly homogeneous group, there were few obvious synapomorphies uniting them. In Fig. 20, although three characters appear as synapomorphies of *Cockerellia*, 2(0), 9(0) and 26(1), two are reversals to the plesiomorphic state and one occurs elsewhere on the tree (26[1] has arisen independently in

Hexaperdita as well). One potential synapomorphy of *Cockerellia,* not included in the analysis, can be seen in the shape of the male genital capsule in lateral view. In all species studied (excluding *P. baileyae*) there are paired, acutely pointed projections on the ventro-medial surfaces of the apices of the gonocoxites (see Figs. 75-90 in Timberlake, 1954).

Because only one species of *Procockerellia* was studied, it is impossible to comment on the monophyly of the group. However, a possible synapomorphy is the deeply divided male sixth sternum with paired apical protuberances clothed in elongate setae (Fig. 21d). *Procockerellia* and *Cockerellia* are united by the shape of the male S7 (6[3]) and the unique male tarsal claw pattern (15[1]).

It is clear from this analysis that the subgenus *Perdita,* represented in Figs. 18-20 by the Halictoides, Ventralis, Sphaeralceae, Octomaculata and Zonalis groups, is not monophyletic. Although some of the species groups within *Perdita* s. str. (e.g., Halictoides and Octomaculata groups) are likely to be monophyletic, the subgenus as a whole is made paraphyletic by the *Cockerellia* group.

Placement of the Subgenus *Xeromacrotera*. The placement of the subgenus *Xeromacrotera* is problematic because this subgenus is known only from the males of *P. cephalotes.* Therefore, many of the characters are unknown for this subgenus, and, in the initial analysis, it was left out. Based on overall appearance and size, *P. cephalotes* appears closely related to *Procockerellia* and/or *Allomacrotera.* However, *P. cephalotes* lacks the derived tarsal claw pattern which unites *Cockerellia* and *Procockerellia* (15[1]) and lacks the reduced number of maxillary palpal segments shown by *Pentaperdita, Procockerellia* (5-segmented) and *Allomacrotera* (3-segmented). Timberlake considered this species to be closely related to *Pentaperdita* because "the maxillary palpi tend to be five jointed" (1954:412). The one male whose mouthparts I dissected clearly has 6-segmented maxillary palpi.

In order to make a preliminary hypothesis of the relationships between *Xeromacrotera* and the other *Perdita* subgenera, I included *Xeromacrotera* in a second analysis of the subgeneric data matrix (Table 2). In this analysis characters were treated as in the first analysis. Using the m*, bb* options of Hennig86 I found 60 trees of length 79, and a consistency index of 56, as in the original analysis. The same resolutions of the polytomy involving *Glossoperdita,* the Halictoides group, *Perditella,* etc. were found, and the trees produced by the two analyses are identical except for the relationships within the *Cockerellia* group. There were 5 equally parsimonious placements of *Xeromacrotera* (Fig. 22a-e). The consensus tree of these five equally parsimonious resolutions is shown in Fig. 22f.

Based on the analysis, *Xeromacrotera* clearly belongs to the monophyletic *Cockerellia* group, which is united by male characters 7(2) and 11(2) and female characters 12(1) and 16(2). The placement of *Xeromacrotera* at the base of this group is essentially determined by three characters. Characters 7(2) and 11(2) place *Xeromacrotera* within the monophyletic *Cockerellia* group and the possession of six-segmented maxillary palpi requires that this species be allied to the basal members of the clade (*Callomacrotera* and *Hexaperdita*), which retain the plesiomorphic, six-segmented condition.

The variable placement of *Xeromacrotera* within the *Cockerellia* group is due more to lack of data than to conflicting characters. This is indicated by the fact that of the seven characters responsible for altering the topology of the trees shown in Fig. 22 (characters 9, 12, 16, 18, 21, 25) all are unknown for *P. cephalotes.*

PHYLOGENETIC RELATIONSHIPS AMONG SPECIES IN THE *MACROTERA* GROUP OF SUBGENERA

Having established the monophyly and the position of the four subgenera *Macrotera, Macroteropsis, Cockerellula* and *Macroterella,* I present a phylogeny of the 31 species in these four subgenera. A revised classification is presented, based on this phylogeny, along with a key to species and diagnoses of species and subgenera.

Table 3 lists the species included in this study, based on Timberlake's classification, and a revised classification, based on results presented below.

DATA MATRIX

The data matrix for this analysis is shown in Table 4. The first three taxa are outgroups. "Panurginae" refers to the non-*Perdita* Panurginae used as outgroups in the subgeneric phylogeny. A second outgroup taxon, "*Perdita,*" represents the members of *Perdita* which belong to the "higher *Perdita*" discussed above. Finally, *P.* (*Pseudomacrotera*) *turgiceps* was included as an outgroup, because, although this species does not belong to the groups here treated, it is clearly near the base of the *Perdita* phylogeny, and is useful for character polarization.

The remaining 27 taxa listed in Table 4 are members of the ingroup. Although there are a total of 31 species in this group (see species diagnoses), 4 species are known only from female specimens, and hence could not be included in the phylogenetic analysis because of lack of data. It was nevertheless possible to place them within the classification based on female characters.

As in the subgeneric data matrix, plesiomorphic character states are all coded 0. For those characters which could not be polarized based on outgroup comparison, the ancestral character state was coded as unknown (? in the data matrix). *P. seminigra* is known only from the holotype male, so female characters are missing for this species.

CHARACTER DESCRIPTIONS

(0) Female paraglossae slender basally but broadening apically to form broad, brush-like apex; **(1)** paraglossae slender and acutely pointed to moderately broad and parallel-sided.

This character was used in the subgeneric analysis (character 1).

2(0) Outer groove of mandible as in most bees, a narrow groove apically but basally broadening to form the outer interspace; **(1)** outer groove of mandible remains discrete basally and extends di-

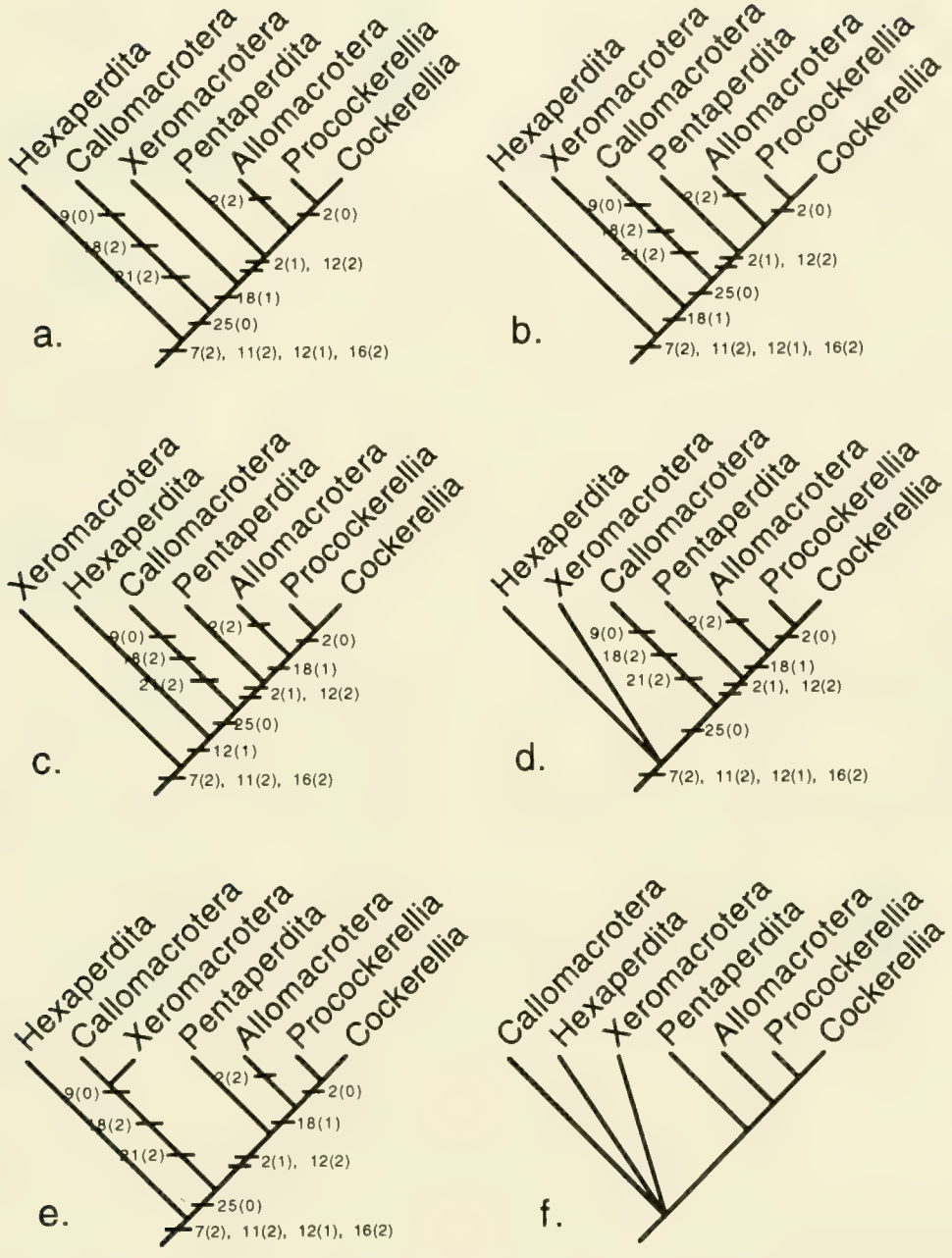


Fig. 22 a-f. Five equally parsimonious placements of the subgenus *Xeromacrotera* **(a-e)**; and the consensus tree of these five trees **(f)**.

agonally across mandible to acetabulum, forming discrete outer mandibular sulcus (present in both sexes).

This character was used in the subgeneric analysis (character 10).

3(0) Pre-episternal groove present and not extending to scrobe or absent; **(1)** Pre-episternal groove plus scrobal groove together forming c-shaped sulcus extending from upper edge of the mesepisternum (below the forewing articulation) to scrobe.

This character was used in the subgeneric analysis (character 5).

4(0) Maxillary palpus relatively long; distal segments (segments 3 to end) subequal to, or slightly shorter than, proximal segments and all segments distinct (Fig. 27); **(1)** Maxillary palpus relatively short due to greatly foreshortened distal segments (Fig. 36a,b).

All non-*Perdita* outgroups possess state 4(0). Within *Perdita* some groups (e.g. *Pentaperdita, Procockerellia* and the *Halictoides* group of *Perdita* sensu strictu) have reduced maxillary palpi, but the distalmost segments are not conspicuously foreshortened relative to the basal segments.

5(0) In females, maxillary palpus 6-segmented (Fig. 27, 36a,c,d);

Table 3. Classification of the basal clade of *Perdita*.

Timberlake (1954-1980)	This paper
Macrotera Smith	*Macrotera*
bicolor Smith (type sp.)	*bicolor* (type sp.)
crassa Timb.	*crassa*
texana texana (Cresson)	*texana* (=*secunda*, *ablusa*)
texana ablusa Timb.	
secunda Ckll.	*sinaloana*
sinaloana Timb.	*pipiyolin* Snelling & Danforth
	nahua Snelling & Danforth
Macroteropsis Ckll.	*Macroteropsis*
anthracina Timb.	*arcuata*
arcuata arcuata Fox	*echinocacti* (=*tepicensis*)
arcuata dinognatha Ckll.	*latior* (type sp.)
atrella Timb.	*magniceps*
echinocacti Timb.	*portalis*
haplura Ckll.	*haplura*
latior Ckll. (type sp.)	
magniceps Timb.	
parkeri Timb.	*Cockerellula*
peninsularis Timb.	*anthracina*
portalis Timb.	*azteca*
robertsi Timb.	*bidenticauda*
tepicensis Timb.	*knulli*
	laticauda
Cockerellula Strand	*lobata*
azteca Timb.	*opuntiae* (type sp.)
bidenticauda Timb.	*solitaria* (=*atrella*, *quadridentata*)
knulli Timb.	*peninsularis*
laticauda Timb.	*rubida*
lobata Timb.	*parkeri*
opuntiae Ckll. (type sp.)	*robertsi*
quadridentata Timb.	*seminigra*
rubida Timb.	
seminigra Timb.	
Macroterella Timb.	*Macroterella*
carinata Timb.	*carinata*
mortuaria Timb. (type sp.)	*mortuaria* (type sp.)
mellea Timb.	*opacella*
nigrella Timb.	*tristella*
opacella Timb.	*nigrella*
tristella Timb.	*mellea*
pilonotata Timb.	
solitaria Ckll.	

Table 4. Data Matrix for characters of species in the *Macrotera* group.

Character numbers	000000000111111111122222222223333
	123456789012345678901234567890123
PANURGINAE	00000000?000?00?0000000000?000000
PERDITA	10100000?000?00?00?00000000000000
PSEUDOMACR.	00100000000020000000000000000000
AZTECA	01000000010101101000000110111000
BIDENTICAUDA	01000000000101101000000010110000
KNULLI	01000000010101101000000110141000
LATICAUDA	01000000010101101000001010130100
LOBATA	01000000010101101000001010130100
OPUNTIAE	01000000000001101000000110120010
PARKERI	01000000000001101000000110120010
BICOLOR	01000000201000011000000000100000
CRASSA	01000000201000011100000000100000
TEXANA	01000000201000011100000000100000
PIPIYOLIN	01000000201000011000000000100001
NAHUA	01000000201000011000000000100001
CARINATA	01000010000000101011000001000000
MELLEA	01000010000000001000000000000000
MORTUARIA	01000010000000101011000001000000
NIGRELLA	0100000?000000001010000000000000
OPACELLA	01000010000000101011000001000000
SOLITARIA	01000010000001101000000010120010
ARCUATA	0101110100000010?000000101000000
ECHINOCACTI	01010101100000101000000010100000
HAPLURA	01011100000110101000110010100000
LATIOR	01011101100000101000000010100000
MAGNICEPS	01011101000000101000000010100000
PORTALIS	01011100000010101000110010100000
TRISTELLA	01000010010000101010000000000000
RUBIDA	01000000000101101000000010101000
SEMINIGRA	?1000000000?011010??000?101200101

(1) maxillary palpus with less than 6 segments; as few as 3 in some species (Fig. 36b).

All non-*Perdita* outgroups possess state 5(0). However, other groups within *Perdita* show palpal segment reduction. Because these groups appear to be distantly related to the *Macrotera* group, palpal reduction is thought to be convergent and the primitive state for *Perdita* is coded 5(0).

6(0) Second labial palpal segment arising apically on first (Figs. 36c,d); **(1)** second labial palpal segment arising subapically on first (Fig. 36a,b).

Character 6(0) is present in all outgroups except *Callonychium mandibulare*, and is therefore considered plesiomorphic for *Perdita*. Furthermore, the apex of the first segment of the labial palpus in those species of *Perdita* in which the second segment arises subapically is acutely pointed while in *C. mandibulare* it is blunt and quadrate apically. This observation suggests that the subapical placement seen in *Perdita* and *C. mandibulare* are not homologous.

7(0) First labial palpal segment longer than (usually two or more times as long as) remaining segments combined (Figs. 27b,d); **(1)** first labial palpal segment roughly equal to or shorter than remaining segments combined (Figs. 27c, 36d).

All non-*Perdita* outgroups studied except *Panurginus occidentalis* and *Heterosarus illinoensis* have character 7(0), which is considered plesiomorphic for *Perdita*.

8(0) Sclerotized rods on sides of aedeagus lacking setae; **(1)** small patches of stout setae on lateral surfaces of aedeagal sclerotization (penis valves) (Fig. 37d, 38e, 39c).

All outgroups possess 8(0). It is often necessary to pull the aedeagus out of the genital capsule to see this character.

9(0) Male T7 lacking discrete pygidial area apically (Figs. 32c, 33c, 34c); **(1)** male T7 with raised pygidial area apically, separated from surrounding cuticle by parallel, acute carinae (as in *P. echinocacti;* Fig. 38c); **(2)** triangular pygidial area apically (as in *P. bicolor*).

Because this character was variable both in the non-*Perdita* and *Perdita* outgroups it was treated as unpolarized.

10(0) Male S1 unmodified (Fig. 60a,b); **(1)** male S1 with apical margin produced into pucker-like lobe (Fig. 61a).

All outgroups had unmodified male S1.

11(0) Glossa not more than twice length of prementum, in some cases less than length of prementum (Figs. 27a-c); **(1)** glossa two or more, usually three, times length of prementum (Fig. 27d).

Glossa length was measured from the glossal sclerite to the tip of the glossa, and prementum length was measured from the base, at the junction with the postmentum, to the point of attachment of the labial palpi (Fig. 27d). Although the derived state is found in the subgenus *Glossoperdita*, all other outgroups studied have state 0, which is therefore considered the plesiomorphic condition of the *Macrotera* group.

12(0) Female S6 with lateral margin unmodified (Fig. 46b, 48a, 49a); **(1)** female S6 with posteriad directed process from latero-apical corner (Fig. 47a, 51a, 52a).

The unmodified state was present in all outgroups. *P. portalis* may represent an intermediate condition but has been coded 12(0).

13(0) Apical portion of male S8 (portion beyond lateral apodemal arms) about equal in width to the basal portion (as in Fig. 48c); **(1)** apical portion of male S8 much broader than basal portion, S8 appearing spade-shaped, apodemal arms indistinct (Fig. 42e, 44d); **(2)** apical portion of S8 broad and protuberant ventrally (Fig. 116-117; Timberlake, 1954).

Because the overall morphology of the male S8 is highly variable among outgroup taxa I was unable to polarize this character. However, 13(2) is clearly an autapomorphy of *P. turgiceps*.

14(0) Distinct latero-apical projection on gonocoxite lacking; **(1)** latero-apical projection present on gonocoxite (as in Figs. 46f, 47f, 48f, 49d, 51g).

Although variously shaped latero-apical gonocoxal projections are present on some other members of the ingroup (e.g., *P. mellea*, Fig. 28f; *P. turgiceps*) and also in many of the outgroups, the state seen in those taxa coded 14(1) appears not to be homologous to the state seen in any outgroup taxa.

15(0) Anterior margin T7 concave or straight in dorsal view (Fig. 28e, 29e); **(1)** anterior margin T7 convex in dorsal view (Figs. 46e, 47d, 52c).

All outgroups possess the concave or straight condition.

16(0) Forewing length less than or equal to 4.5 mm; **(1)** forewing length greater than 4.5 mm, usually around 5.0 mm.

The polarity of this character is not known because of variability in the outgroups.

17(0) Hind tibia of males with erect, fine setae, not conspicuously branched or thick; **(1)** hind tibia of males with stout, erect, moss-like setae on outer surface.

All outgroups possess state 17(0). Timberlake (1954) used this character in the key to subgenera.

18(0) Male face with yellow maculation; **(1)** male face lacking yellow maculation, though the mandibles may be yellow.

All non-*Perdita* outgroups studied have yellow on the faces of males, so the absence of yellow coloration is considered derived.

19(0) Female mandible with pre-apical pollex; **(1)** female mandible simple, lacking pollex.

All non-*Perdita* outgroups possess simple female mandibles, while in *Perdita* the state is variable.

20(0) Female mesonotum with conspicuous, erect, finely-branched setae; **(1)** female mesonotum with widely scattered, very short, recumbent setae visible only under high magnification (> 60x).

All outgroups possess at least some elongate mesonotal setae.

21(0) Male facial fovea small depression lined with fine setae, as in most andrenids; **(1)** male facial fovea large, slightly protruding, with glandular tissue visible beneath cuticle (Fig. 42b).

Facial foveae in bees and sphecid wasps have been shown to be glandular structures based on histological sections (Duffield et al. 1984; Heselhaus 1922; Nedel 1960; Schönitzer & Schuberth 1993; Schuberth & Schönitzer 1993), but the function of these glands is unknown. All outgroups studied had small inconspicuous male facial foveae, similar to those of females. In *P. portalis* and *P. haplura*, however, the facial foveae are large and convex, with glandular tissue visible through the cuticle. In dissections of male *P. portalis* these structures were pale cream color and were sandwiched between the outer cuticle and an inner layer of thin cuticle.

22(0) Apical margin of male clypeus, where labrum attaches, concave or straight (Fig. 28b, 29b); **(1)** male clypeus overhanging labrum slightly and acutely pointed apically, especially in the larger-headed specimens (Fig. 42b).

All non-*Perdita* outgroups lack the acutely pointed clypeus. Almost all other species of *Perdita* investigated have a concave clypeal margin but in some species of *Perdita* sensu stricto the clypeus is acutely pointed. Nevertheless, 22(0) is considered plesiomorphic for the *Macrotera* group.

23(0) Volsellar cuspus variable in shape but always small and not extending beyond apex of paramere; **(1)** cuspus enlarged, laterally compressed and extending beyond apex of paramere (Fig. 51g, 52d).

All outgroups possess state (0).

24(0) Lateral surfaces of female propodeum with scattered, finely branched setae; **(1)** two patches of dense, short, finely branched setae on lateral surfaces of female propodeum; setae packed so densely as to obscure the cuticle below.

All outgroups possess state (0).

25(0) Male T6 with fine, erect, scattered setae; **(1)** male T6 with single subapical line of few erect, stout, finely branched setae (Fig. 38c, 51c).

Timberlake referred to these as "moss-like" setae (1954:352). All outgroups possess state 25(0).

26(0) Male T7, as in most bees, with lateral margins not meeting ventrally (Figs. 37c, 38d); **(1)** male T7 forming tube due to reflexed lateral margins, which almost touch ventrally (Fig. 32c, 33c, 34c).

All outgroups possess state (0).

27(0) Lateral graduli of male T2 and T3 lacking; **(1)** lateral graduli present on T2 and/or T3 in males (Fig. 1a,b).

Tergal graduli extend completely across the male T2 and T3, ending at the lateral margins of the terga, in most species of *Perdita*. However, in some species (e.g., *P. texana*), near the lateral edges of the terga the graduli turn posteriorly and run parallel to the long axis of the body. These lateral portions of the graduli are referred to as the lateral graduli. In the non-*Perdita* outgroups studied this character varied, with most Calliopsini possessing lateral graduli and the Melitturgini, Panurgini and Protandrenini lacking lateral graduli. I have coded this character as variable (?) for the non-*Perdita* outgroups and (0) for the *Perdita* outgroups.

28(0) Male S2 and S3 unmodified (Fig. 61a); **(1)** male S2 and S3 with broad, obtuse protuberances along posterior margins, strongest in S3 (Fig. 62a); **(2)** male S2 with quadrate protuberance which projects over surface of S3 (Fig. 62b); **(3)** male S3 with discrete, rectangular patch of stout setae (Fig. 62c); **(4)** S2 with paired diverging ridges along posterior margin.

All outgroups possess unmodified male second and third sterna.

29(0) Penis valves variable, but not connected dorsally by slender bars of cuticle; **(1)** penis valves connected dorsally by slender cuticular bars (Fig. 46f, 48f, 49d).

All outgroups have state (0).

30(0) Apical margin of male T7 variable in shape; **(1)** apical margin of male T7 dorso-ventrally flattened, forming a broad horizontal shelf with widely separated, acute corners (Fig. 51e, 52c).

All outgroups possess state (0).

31(0) Penis valves parallel; **(1)** penis valves divergent (Fig. 54f, 55d, 56b, 57f).

All outgroups possess state (0).

32(0) Volsella highly variable in shape, but not as in alternative state; **(1)** volsella chelate, as in a crab claw, with apex of cuspis acute and strongly recurved.

The volsellae are highly variable in shape among species of *Perdita*. *P. nahua* and *P. pipiyolin* are unique in possessing a stout, acutely pointed and apically recurrent cuspis.

33(0) Apical margin of male T7 variable in shape; **(1)** apical margin of male T7 produced at corners into elongate acute prongs, separated by deep emargination (Figs. 55c, 56c,d).

All outgroups possess state (0).

PHYLOGENETIC ANALYSIS

The m*, bb* options of Hennig86 resulted in four equally parsimonious trees of length 46 and consistency index = 82 for the 33 characters and 29 taxa listed in Table 4. Characters were all treated as unordered. The Hennig86 ie (implicit enumeration) command resulted in the same 4 trees. Figure 23 shows the consensus tree, Fig. 24a-d show the 4 equally parsimonious resolutions, and Fig. 25 shows the characters mapped onto the preferred tree. Fig. 26 shows the preferred tree and the limits of the four subgenera.

TREE TOPOLOGY AND RELATIONSHIPS AMONG SPECIES.

The monophyly of the *Macrotera* group of subgenera is supported in the present analysis. Both characters 2(1) and

Fig. 23. Consensus tree of species-level analysis. "Panurginae" refers to the panurgine genera used as outgroups in the subgeneric phylogeny. "*Pseudomacrotera*" refers to the monotypic subgenus which includes *P. turgiceps*. While this species does not belong to the groups here treated, it is clearly near the base of the *Perdita* phylogeny, and is useful for character polarization. "*Perdita*" represents all the other species of *Perdita* (referred to in the text as the "higher *Perdita*").

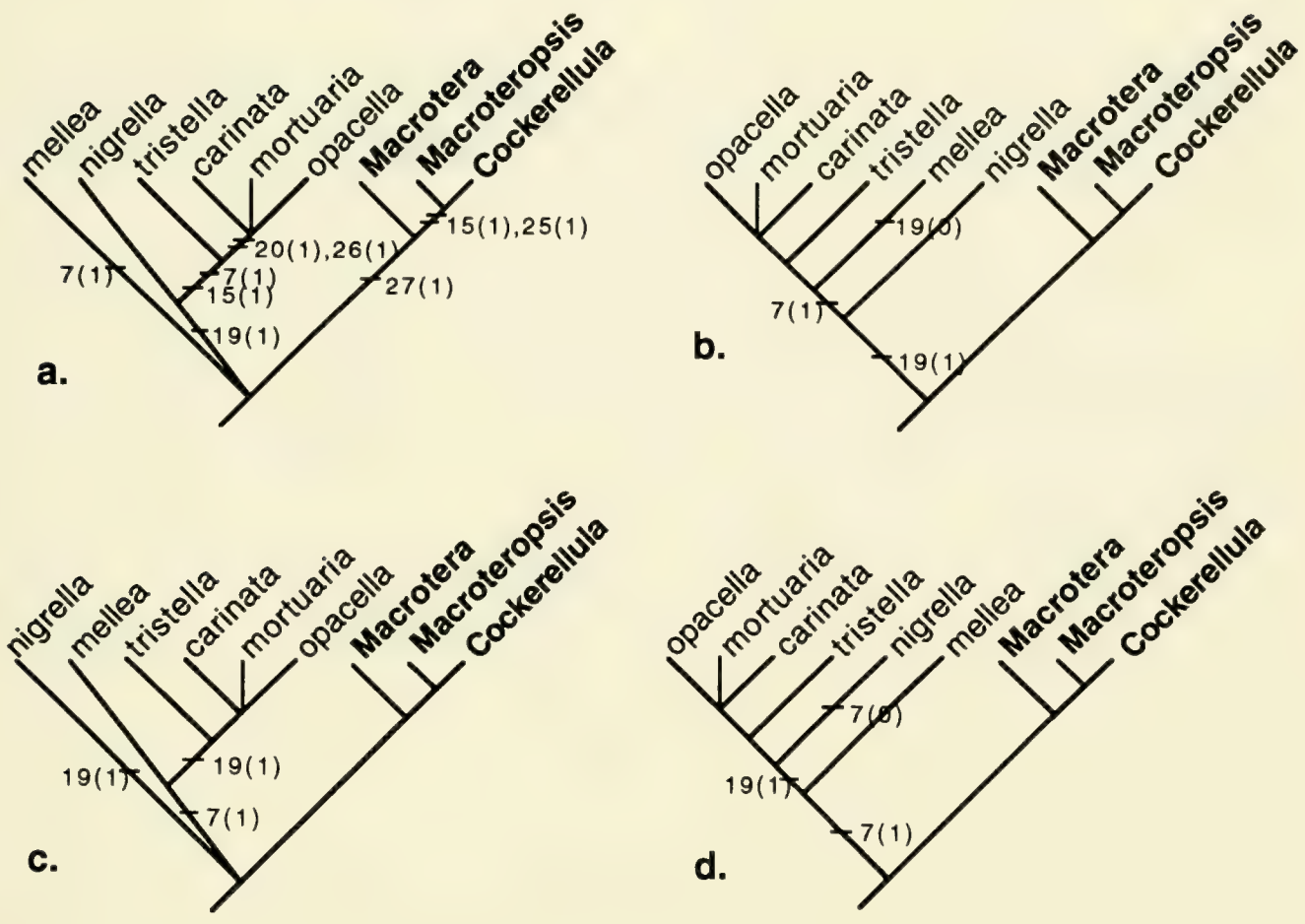


Fig. 24. Four equally parsimonious resolutions of basal polytomy in the consensus tree (Fig. 23).

17(1) unite all four subgenera, excluding the remainder of *Perdita* (Fig. 25).

The primary source of ambiguity in this analysis involves the relationships among the basal species, the members of Timberlake's subgenus *Macroterella* excluding *P. solitaria*, which clearly belongs elsewhere (see below). In two of the four resolutions, *Macroterella* (*P. mellea, P. opacella, P. carinata, P. mortuaria, P. tristella* and *P. nigrella*) appears monophyletic (Fig. 24b,d), while in two others the group is potentially paraphyletic (Fig. 24a,c). The ambiguity arises from the incongruity of characters 7 and 19. I prefer the resolution in which the ci of character 19 is maximized (ci=100, Fig. 24a,d), at the expense of character 7. The tree shown in Fig. 24a seems the most likely, indicating the possibility that *P. mellea* does not belong to a monophyletic *Macroterella*.

On a more positive note, the monophyly of *P. carinata, P. opacella* and *P. mortuaria* is well supported by characters 20(1) and 26(1), and the placement of *P. tristella* as the sister group to these three species is supported by character 15(1), although this character arises in parallel higher up in the tree (Fig. 25). This group of four species all have very similar genital capsules (Figs. 31f, 32d, 33d, 34d).

The monophyly of the subgenera *Macrotera, Macroteropsis* and *Cockerellula* is supported by 27(1), the presence of conspicuous lateral graduli on male T2 and T3.

The monophyly of the subgenus *Macrotera* is supported by the elongate glossa (11[1]), large body size, as measured by forewing length (16[1]), and the distinctly shaped male pygidial plate (9[2]). Although the relationships within this group are not fully resolved, the sister group relationships between *P. crassa* and *P. texana*, and *P. pipiyolin* and *P. nahua* are clear.

The characters uniting the subgenera *Macroteropsis* and *Cockerellula* are the shape of the anterior margin of the male T7 (15[1]) and the presence of a subapical band of erect, coarsely-branched setae on the male T6 (25[1]).

The composition of these two subgenera has been changed somewhat as a result of the present analysis. *Macroteropsis* now refers to a group of 6 species united by characters 4(1), 5(1) and 6(1). Although Timberlake considered reduced maxillary palpi one of the defining characters of *Macroteropsis* (Timberlake, 1954:356), he included several species which did not show such palpal reductions. Other characters listed as diagnostic of the subgenus are common to other groups or are

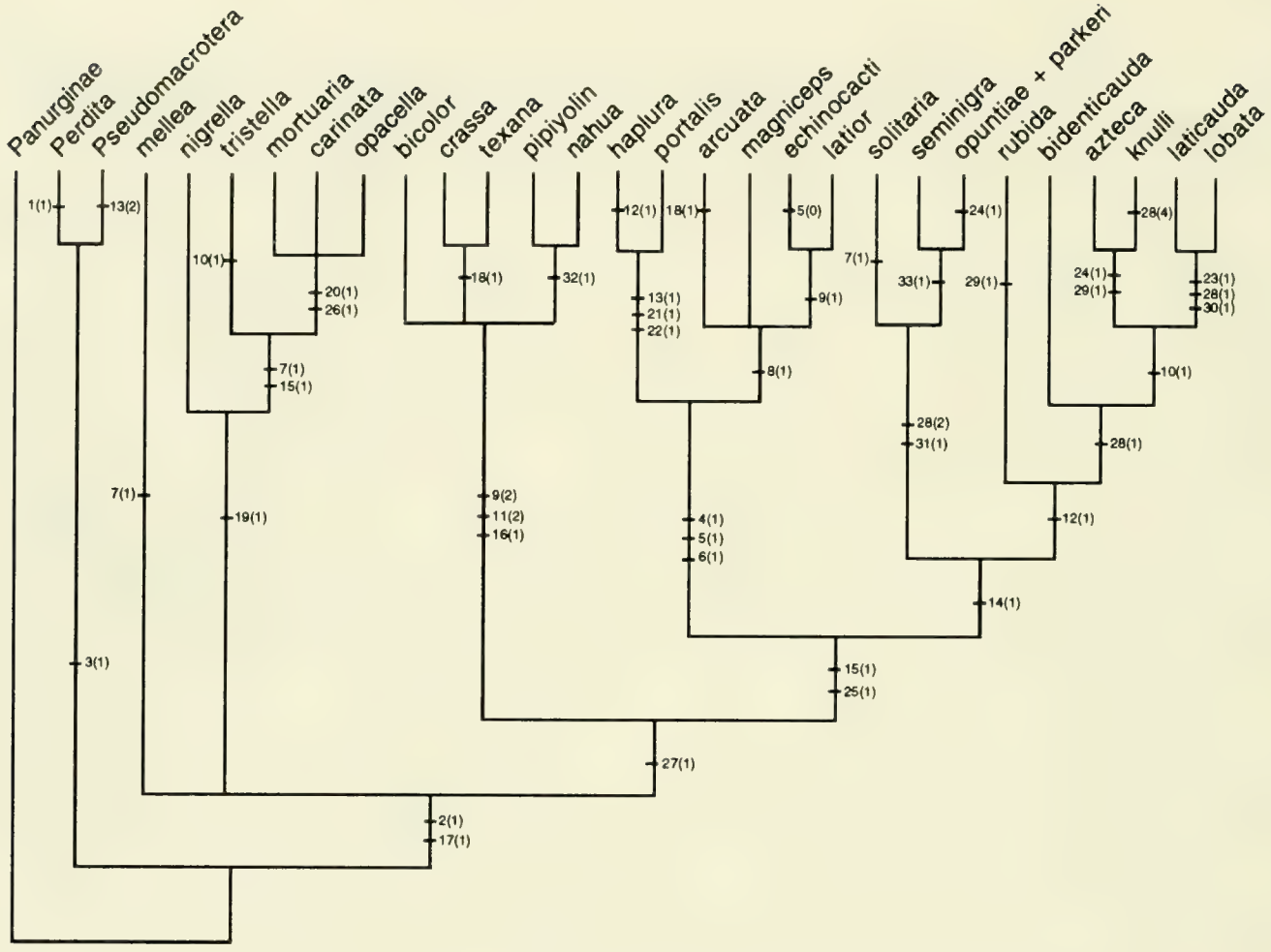


Fig. 25. Preferred tree with characters mapped on. See explanation of outgroup taxa in caption to Fig. 23.

highly variable. He did not mention the maxillary palpal character (6[1]) which I have included.

The monophyletic group united by character 14(1) is an expanded subgenus *Cockerellula*. *P. solitaria* had previously been placed in *Macroterella*, but there is little doubt that it is closely related to *P. opuntiae* and its relatives. Although in the cladogram *Cockerellula* is united by a single male character (14[1]), it was possible to place some species known only from females (e.g., *P. peninsularis*, *P. anthracina*) with certainty in *Cockerellula* based on female characters included in the analysis (e.g., 12[1]).

Classification

Timberlake's classification of the group and a modified classification, based on the phylogenetic analysis, are shown in Table 3. The subgenus *Macrotera* remains essentially unchanged, except for the addition of two new species and some synonymy. The subgenus *Macroteropsis* has been reduced in size as a result of synonymy (e.g., *P. tepicensis*) and the transfer of some species to *Cockerellula*. *Cockerellula* includes more species than previously.

Timberlake's subgenus *Macroterella* has been changed considerably as a result of this study. *P. pilonotata* clearly belongs to the distantly related subgenus *Heteroperdita*, and, as a result of finding the male of *P. solitaria*, this species has been transfered to *Cockerellula*. Although ambiguity about the relationships among the remaining species of *Macroterella* (*P. mellea*, *P. nigrella*, *P. tristella*, *P. carinata*, *P. opacella*, and *P. mortuaria*) persists, there is no convincing reason to split this group up further. Although in some of the resolutions (Fig. 24) *Macroterella* is potentially paraphyletic, in others it is monophyletic. One species, *P. mellea*, is highly autapomorphic (see below) and one could, based on phenetic grounds, place this species in its own subgenus in order to call attention to its autapomorphic features, but at present this seems unnecessary.

Diagnosis of the *Macrotera* Group of Subgenera

The four subgenera treated below can be recognized by the following characters: (1) mandible with discrete, well impressed sulcus on outer surface running from acetabulum diagonally across base and then along lower, or condylar, mar-

Fig. 26. Preferred tree showing limits of subgenera. See explanation of outgroup taxa in caption to Fig. 23.

gin, (2) paraglossae in females slender basally and expanded into a broad, brushlike apex, (3) scrobal sulcus lacking, (4) male with highly variable head shape due to positive allometry in several aspects of head capsule, but in general head broad and quadrate, (5) yellow maculation usually absent on the meso or metasoma, and (6) male usually with reddish metasoma.

KEY TO THE SPECIES OF THE *MACROTERA* GROUP

1. Large bees (forewing length 4.5 mm or more); glossa 2-3 times length of prementum (*Macrotera*) . . . . . . see Snelling & Danforth (1992) for a key to species
— Smaller bees (forewing length 4.0 mm or less); glossa no more than 2 times length of prementum and usually about equal to length of prementum 2
2. Second segment of labial palpus arising subapically on first segment, first segment acutely pointed apically; maxillary palpal segments 3 and beyond greatly shortened and sometimes lacking, such that palpi 4 to 6-segmented; head of female broad, width 1.3 times length (*Macroteropsis*) 9
— Second segment of labial palpus arising apically on first segment; maxillary palpus 6-segmented; segments subequal in length; head of female usually rather slender, width 1.1 times length 3
3. Female with extensive yellow maculation on head and mesosoma, metasoma reddish orange; male uniformly reddish orange with yellow maculation on lower part of face; forewing length 1.8-2.3 mm. . . . . .*P. mellea*
— Female head and mesosoma primarily black (yellow on mandible, lower part of frons and foreleg in some species); male head and mesosoma primarily black (except for some yellow on the clypeus and supraclypeal area); forewing length usually greater than 2.5 mm 4
4. Female mandible simple; metasoma black; small bees without conspicuous erect setae; male T6 and T7 lacking mosslike setae; no graduli visible on lateral corners of T2 and T3; S8 not very slender; genital capsule without latero-apical processes (*Macroterella,* in part) 5
— Female mandible with pollex; metasoma usually reddish; some species with dense patches of setae on lateral surfaces of propodeum; larger bees; males with conspicuous moss-like setae on T7 and in a single row across T6; graduli visible on lateral corners of T2 and T3; S8 long and slender; genital capsule with lateroapical processes (*Cockerellula*) 14
5. Male T7 tubelike, lateral portions almost touch ventrally; female lacking erect setae on mesonotum but

with yellow maculation on anterior surface of foretibia 6
— Male T7 not tubelike; females with a few erect setae on mesonotum and no yellow maculation on foretibia 8
6. Male T7 divided medially by slit flanked by two postero-laterally directed prongs; female with relatively broad and obtuse pygidial plate; metallic tinge on frons and vertex distinctly greenish ..... *P. opacella*
— Male T7 not divided medially and lacking prongs; female with relatively slender, acutely pointed pygidial plate; metallic tinge on frons and vertex weak and coppery in coloration 7
7. Male T7 with longitudinal carina at apex ... *P. carinata*
— Male T7 simply tubelike, without apical modifications ..... *P. mortuaria*
8. Female facial fovea slender and deeply impressed (length 5-6 times width); frons more shiny with less greenish tinge; basitibial plate poorly defined, represented by an acute prong on posterior margin of tibia; female S6 only weakly emarginate apically (depth of emargination less than width); male with yellow restricted to clypeus, with very faint yellow on area of frons just lateral to clypeus, between clypeus and eye; male S1 lacking acute prong along posterior margin; S7 spatulate ..... *P. nigrella*
— Female facial foveae broader (length 3 times width); frons more tesselate, greenish tinge more evident; female basitibial plate distinctly raised and well defined all around; female S6 deeply emarginate apically (depth of emargination greater than width), male with more extensive yellow maculation, yellow on face below level of antennal sockets; male with median, acute prong arising from the posterior margin of S1; S7 gradually tapering to acute apex ..... *P. tristella*
9. Maxillary palpi 5- to 6-segmented; wings hyaline with brownish wing veins; facial maculation restricted to below level of antennal sockets in male; aedeagus with small patches of stout setae on each side 10
— Maxillary palpi 4-segmented; wings cloudy whitish with pale brown veins; yellow on face extending up above level of antennal sockets in male, often to vertex, or head entirely orange-ferruginous; aedeagus lacking stout setae 12
10. Male pygidial plate lacking; male mandible simple; S8 of male rather broad apically; clypeus with transverse ridge; female with broad, transparent area on S6 (length 2-3 times width); lateral surfaces of propodeum with erect, white setae ..... *P. arcuata*
— Male pygidial plate formed by two parallel carinae at apex of T7; male mandible bidentate; S8 of male slender and not expanded apically; clypeus flat; female with more slender transparent area on S6 (length 5-6 times width); lateral surface of propodeum with only a few scattered, white setae 11
11. Male with protuberance at midpoint of S2; female with conspicuous bluish tinge; maxillary palpus distinctly 6-segmented ..... *P. echinocacti*
— Male without protuberance at midpoint of S2; female with more greenish tinge; maxillary palpus 6-segmented but segment 5 very difficult to distinguish ..... *P. latior*
12. Male head entirely ferruginous, with yellow maculation below level of antennal sockets; mesosoma and metasoma partly ferruginous; female with dense, closely-appressed white setae over scutum and scutellum; orange-ferruginous maculation over at least lower portion of clypeus, surrounding compound eye and extending medially along vertex to lateral ocellus ..... *P. magniceps*
— Male head yellow or orange ferruginous up to level of ocelli, becoming dark brown across vertex; genal width subequal to width of compound eye; mesosoma and metasoma mostly dark brown 13
13. Male facial fovea large, pale cream colored and seemingly glandular; T7 rather slender apically (apex 0.2 mm in width) and without conspicuous latero-apical prongs; female eyes weakly convergent below (Fig. 42a); female foretibia with yellow maculation; pygidial plate narrow and acute (Fig. 42d) .... *P. portalis*
— Male facial fovea large and black, not noticably glandular; T7 broader, more obtuse apically (apex 0.55 mm in width) and with two small prongs on either side of broad, convex apical margin; female eyes strongly convergent below (Fig. 44a); female foretibia without yellow maculation; pygidial plate broader and obtuse (Fig. 44c) ..... *P. haplura*
14. Females 15
— Males 24
15. Metasoma primarily black or deep brown 16
— Metasoma reddish 19
16. Blue-green metallic tinge to head and mesosoma ..... P. *rubida*
— Very weak, if any, metallic coloration 17
17. Female robust, with long erect white setae over head and mesosoma; wing veins dark brown; pygidial plate gently rounded and obtuse apically ..... *P. anthracina*
— Female more slender and with shorter, less conspicuous white setae; wing veins light brown; pygidial plate acutely pointed and slender 18
18. Labial palpal segments 2-4 elongate and slender, equal in combined length to segment 1; S6 not notched apically; forewing length less than 3.0 mm . *P. solitaria*
— Labial palpal segments 2-4 shorter, their combined length less than that of segment 1; S6 strongly notched apically; forewing length greater than 3.0 mm ..... *P. peninsularis*
19. Lateral surface of propodeum with discrete patch of stout white setae, which completely obscures the underlying cuticle 20
— Lateral surface of propodeum with more widely spaced white setae, not forming dense patch; cuticle easily visible through setae ..... *P. laticauda, P. bidenticauda,* or *P. lobata* (males needed for definite identification)
20. Large, robust bees with elevated triangular supraclypeal area extending upward between antennal bases;

mid and hind tibial spurs acutely bent at apex and with long teeth, appearing nearly pectinate; facial fovea elongate and slender (0.41-0.54 mm) ..... *P. azteca*
— Bees of various sizes but lacking elevated supraclypeal area; tibial spurs finely serrate; facial fovea slender, shorter 21
21. Anterior face of T1 brownish, rest of metasoma reddish; dorsal, central surface of propodeum with antero-posterior striae converging posteriorly ..... *P. parkeri*
— Anterior surface of T1 reddish like rest of metasoma; dorsal, central surface of propodeum finely alveolate, no obvious linearity to scupturing 22
22. Yellow maculation on lower part of paraoccular area immediately lateral to clypeus, running just above fronto-clypeal suture from outer subantennal sulcus to base of mandible ..... *P. robertsi*
— Face lacking yellow maculation, except for slight yellow on clypeus and mandible 23
23. Large, robust bees (forewing length greater than 3.5 mm) ..... *P. opuntiae* (or *P. seminigra*)
— Smaller bees (forewing length less than 3.0 mm) ..... *P. knulli*
24. S1 of male with median pucker-like fold (Fig. 61a) ..25
— S1 of male unmodified (Fig. 60a,b) 28
25. S3 of male with median rectangular patch of short, dense setae (Fig. 61c); apex of T7 dorso-ventrally compressed, forming a broad horizontal, roughly quadrate margin 26
— S3 of male without median patch of setae; T7 variable 27
26. Posterior margin of T7 more strongly emarginate medially and lateral corners more pronounced and more strongly bent ventrad (Fig. 52c); papillae on cuspis extend to apex (Fig. 52d) ..... *P. lobata*
— Posterior margin of T7 less strongly emarginate medially and lateral corners more horizontal (Fig. 51f); papillae on cuspis restricted to basal half (Fig. 51g) ..... *P. laticauda*
27. Large, robust bees (forewing length greater than 3.5 mm); mandible simple; bright yellow maculation on mandible, labrum, clypeus and frons below level of antennal sockets; T7 with long, paired, postero-dorsal projections arising subapically ..... *P. azteca*
— Small bees (forewing length less than 3.0 mm); mandible bidentate; creamy white on mandibles, labrum, clypeus and frons below level of antennal sockets; T7 narrowed apically with two small apical prongs ..... *P. knulli*
28. Posterior margin of S2 with median quadrate protuberance extending out of plane of other sterna, over surface of S3, and ending in two sharp points 29
— Margin of S2 with slight thickening or bulge but not extending over surface of S3 32
29. Large bees (forewing length greater than 3.5 mm); apical margin of T7 broadly emarginate with two widely separated, acutely pointed prongs 30
— Small bees (forewing length less than 2.6 mm); T7 quadridentate apically, two median processes directed meso-posteriad, two horizontal processes directed postero-laterad ..... P. *solitaria*
30. Yellow facial maculation extending completely across face below level of antennal sockets (on clypeus, supraclypeal and paraoccular areas); prongs of T7 more widely separated (>0.56 mm) and emargination between prongs u-shaped 31
— Yellow to white facial maculation restricted to paraoccular area, no yellow maculation on clypeus; prongs on T7 less widely separated (<0.48 mm), and emargination between prongs v-shaped ..... *P. seminigra*
31. Mesoscutum shiny with small, widely scattered, but distinct, punctures; head and thorax brownish ... . *P. opuntiae*
— Mesoscutum dull, infuscate, with barely discernible punctures; head and thorax black ..... *P. parkeri*
32. S3 with broad, transverse bulge along posterior margin; S2 with similar, but less prominant bulge; facial maculation creamy white, on lower part of face reaching to upper margin of antennal sockets ..... *P. bidenticauda*
— S2 and S3 unmodified; yellow facial maculation on clypeus, supraclypeal and paraoccular areas, extending upward along inner margins of eyes to facial foveae ..... *P. rubida*

SPECIES DIAGNOSES

Although Timberlake published complete descriptions of most of the species in this group, I have included diagnoses for each species, listing the most useful characters for species-level recognition. Many of these features were not mentioned by Timberlake. Brief descriptions of the geographic distributions and floral host associations are also given. I have included complete descriptions of species which were not adequately described originally and a description of a newly discovered species from Mexico.

In the lists of plant records I have given the plant associations according to plant genus, and included specific names, if given, in parentheses. I have also included the numbers of males and females collected on each plant genus, for those specimens with plant records.

Subgenus *Macroterella* Timberlake

Macroterella Timberlake, 1954:360 [description]; 1954:361 [key to species]; 1956:324 [additional species]; 1960:125 [new records]; 1968:7 [additional keys]; 1980:6 [additional species, new records].

Type species – *Perdita mortuaria* Timberlake, by original designation.

Diagnosis – Members of this subgenus are some of the smallest species in the *Macrotera* group. Features which serve to distinguish this subgenus from all other *Perdita* include: (1) greatly shortened mouthparts, with glossa length usually equal to or less than length of prementum, (2) first labial palpal segment equal in length to remaining segments combined, (3) female mandible simple and acutely pointed (except *P. mellea*).

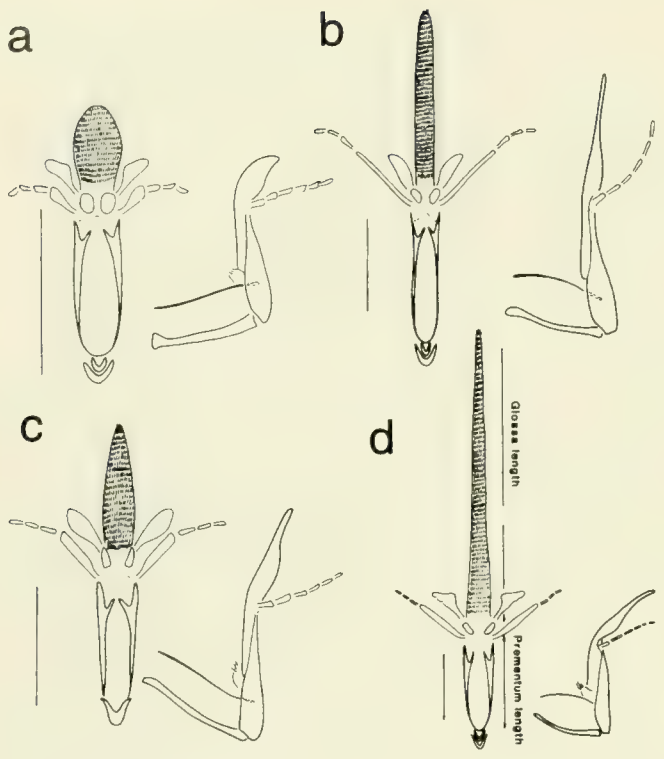


Fig. 27. Mouthpart morphology, females. **(a)** *P. mellea,* **(b)** *P. nigrella,* **(c)** *P. opacella,* **(d)** *P. bicolor* (Scale bar = 0.5 mm, except in *P. bicolor,* in which it equals 1.0 mm).

***Perdita* (*Macroterella*) *mellea* Timberlake**
(Figs. 27a, 28, 30)

Perdita (*Macroterella*) *mellea* Timberlake, 1954:364 [description]; 1954:361 :[key]; 1960:125 [additional material]; 1968:7 [key].

Type material – The holotype male and allotype are located in the CAS (Type No. 14606). Both specimens were collected at Picacho Pass, Pima Co., Arizona, August 7, 1940, on *Euphorbia* (Timberlake, coll.).

Diagnosis – Forewing length 1.8 - 2.3 mm. This species is very distinctive. The male is entirely ferruginous, with erect, white setae over the mesonotum, metanotum, pleura and lateral surfaces of the propodeum, and with yellow maculation on the face up to the level of the antennae. The head is broad with blue-grey eyes (in the normal male morph collected on flowers, see below) and the mandibles are simple. The distinctive male genitalia and apical sterna further distinguish this species. The head and mesosoma of females is black with extensive yellow maculations on the medial and lateral areas of the clypeus, along the midline of the frons from the frontoclypeal suture to the anterior ocellus, from the paraocular areas upward along the inner margins of the eyes to the vertex, and on the scutellum the metanotum and the upper, horizontal surface of the propodeum. The fore and mid legs are yellow beyond the apices of the femora. Females also possess a distinctive type of sculpturing over the mesopleura: although imbricate-punctate, with erect white setae on the lower portion of the mesopleuron, the cuticle is deeply and minutely alveolate on the upper portion. The metasoma is reddish. The mouthparts of *P. mellea* are the shortest of all the species in the *Macrotera* group. The glossa is scarcely longer than wide and considerably shorter than the length of the prementum. The galea and the labial palpi are greatly shortened. The maxillary palpi are six-segmented but also very short.

Like *P. portalis,* males of *P. mellea* are dimorphic (Rozen, pers. comm.). The typical, flight-capable male is described in the diagnosis given above. As there is no published description of the macrocephalic male morph, I present a description of this form below, based on two specimens provided by Dr. Jerome G. Rozen, Jr., AMNH.

Description – MACROCEPHALIC MALE MORPH – Head: (43) greatly expanded compared with flight-capable morph, width 3.2 mm; (44) quadrate, 1.42 times broader than long; head width increases from top to bottom, so that greatest head width is at level of mandibles; (45) clypeus compressed and elongate, ventral projections on either side of labrum enclose labrum as in small-headed male; (46) frons, supraclypeal and paraocular areas shiny with abundant, closely-spaced punctures and fine, white recumbent setae; (47) vertex and entire region above ocelli shiny and without punctation; (48) gena greatly expanded behind eye (maximum width 0.51 mm); glabrous and impunctate down to level of upper margin of eye; below upper margin of eye surface shiny but with numerous, minute punctures; (49) head coloration more or less as in small-headed male, honey yellow over most of head, with yellow to white maculation on face below level of antennae; (50) head, except impunctate regions, clothed in fine white setae; (51) eyes greatly reduced (0.34 mm in length) in comparison to small-headed male, weakly convex and roughly coplanar with surrounding head capsule; eyes black (in pinned specimens); (52) median and lateral ocelli separated by more than one ocellar width; ocelli greatly reduced in size (1/2 size of ocelli in large-headed male) and hardly convex above level of surrounding cuticle; (53) facial fovea very weak, appearing as faint dimples at about level of upper eye margin; (54) scape light yellow as on lower part of face, pedicel and flagella darker yellow, concolorous with head above level of antennae.

Mouthparts: (55) labrum rectangular and pale yellow; glabrous medially with small, weak punctures and fine white setae laterally; (56) mandible stout, and tapering to an acute apex; no preapical tooth; yellow, with reddish tips; (57) glossa short, 1/5 length of prementum and barely longer than wide; (58) paraglossa slender and acutely pointed, roughly equal to glossa in length; (59) labial palpus 4-segmented, first segment shorter than remaining segments combined; (60) galeal comb absent or at least very difficult to see; (61) maxillary palpus 6-segmented, segments short but all distinct, maxillary palpi extend beyond apex of galea. The mouthparts of large-headed males are similar to those of small-headed males but differ from females in that females have broad, brush-like paraglossae.

Mesosoma: (62) pronotum longer (length = 0.32 mm along midline in dorsal view) and far more robust than in small-headed male; dorsal surface divided by transverse groove and lateral surface rather deeply impressed giving rise to distinct dorso-lateral lobes of pronotum; pronotal lobes clothed in white setae; (63) mesoscutum paler and reduced in size relative to small-headed male; dorsal surface essentially flat (far more convex in small-headed male); surface weakly imbricate with scattered erect white setae; (64) mesoscutellum and metanotum in comparison to small-headed male reduced in size and flattened; (65) mesopleuron as in small-headed male, with dense white setae; (66) metapleuron weakly alveolate, lacking setae; (67) propodeum more abruptly declivous than in small-headed male, with same erect white setae separating dorsal and lateral surfaces and similar alveolate sculpturing; (68) intertegular distance 0.51 mm; (69) wings reduced in size;

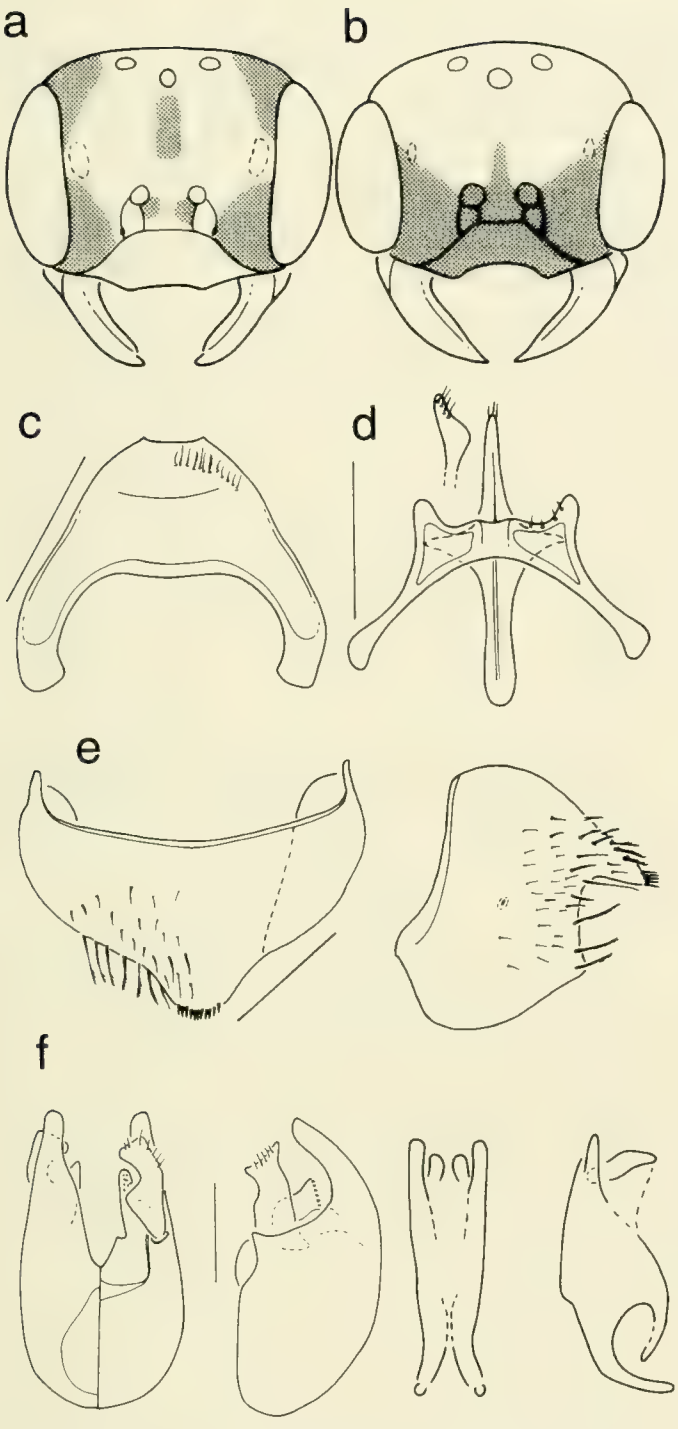


Fig. 28. *Perdita mellea.* **(a)** female head, **(b)** male head, **(c),** female S6, **(d)** male S7 and S8, **(e)** male T7, dorsal and lateral views, **(f)** male genital capsule (dorsal, ventral and lateral views), aedeagus (dorsal and lateral view). In this figure and the following figures, the scale bar lengths are as follows (unless specified differently on the figure): female S6, 0.25 mm; female T6, 0.5 mm; male T6, 0.5 mm; male S7 and S8, male T7, genital capsules, 0.25 mm.

forewing length 1.56 mm (forewing length usually reaches 2.0 mm in small-headed males); (70) legs concolorous with rest of mesosoma except for apices of femora and bases of tibiae, which are pale yellow; (71) basitibial plate slightly smaller than in small-headed male but well-defined; (72) outer surface of hind tibia with erect, finely branched setae; (73) midtibial spur minutely serrate; (74) hind tibial spurs subequal in length and finely serrate; (75) tarsal claws all bifid.

Metasoma: (76) terga concolorous with mesosoma; metasoma overall broader and more dorso-ventally flattened than in small-headed male; (77) T1-T6 clothed in minute, unbranched, appressed setae; (78) T6 with more elongate, erect, but unbranched setae; (79) fovea on T2 present but shallow and weakly developed; (80) pygidial plate lacking on T7, but band of long, erect setae present apically; (81) graduli present on T2-T6 but do not extend far enough laterally and posteriorly to be visible in dorsal view; (82) sterna similar in color to terga; (83) S1-S6 similar in color and vestiture to terga; (84) sternal graduli only present on S1, lacking on all other sterna; (85) S7 and S8 as in small-headed male (Fig. 28d); (86-89) genital capsule as in small-headed male (Figs. 28f).

Distribution – Desertic parts of San Bernardino, Riverside counties, California; Cochise, Pima, Pinal and Yuma counties, Arizona; Hidalgo Co., New Mexico; Presidio Co., Texas; states of Sonora, Baja California Norte and Baja California Sur, Mexico (Fig. 30). Additional specimens are recorded from Chihuahua, Mexico by the Programa Cooperativo sobre la Apifauna Mexicana (PCAM) (Ayala, et al., 1996), but I have not examined these specimens myself.

Phenology – July through October.

Floral associations – The vast majority of specimens were collected on *Euphorbia* (*polycarpa, polycarpa* var. *hirtella, albomarginata hirtella*) (89 females/32 males) with some specimens on *Eriogonum inflatum* (2 females/0 males).

Perdita (Macroterella) nigrella Timberlake

(Figs. 27b, 29, 30)

Perdita (*Macroterella*) *nigrella* Timberlake, 1954:362 [description]; 1954:361 :[key]; 1968:7 [key].

Type material – The holotype male is located in the CAS (Type No. 14631). The holotype and allotype were collected along Artist Drive, West side of Death Valley, Inyo Co., California, April 7, 1939, on *Phacelia* (E.G. Linsley, coll.).

Diagnosis – Forewing length 2.6 to 3.0 mm. This species, like the following one, can be distinguished from other members of the subgenus by the presence of scattered, erect setae on the scutum of both males and females. Females are mostly black with a slight greenish metallic hue on the head and scutum and yellowish mandibles, becoming fuscous apically. There is no yellow coloration on the foretibia. In females, the facial foveae are slender and the basitibial plate is unusual in that it does not have a clearly defined rim separating it on all sides from the remainder of the tibia. Rather, the basitibial plate forms an acute projection off the posterior margin of the tibia. Females of this species are further distinguished by the shape of S6. Males have large, quadrate, mostly black heads with yellow restricted to the clypeus and the paraocular areas, below the upper margin of the clypeus. The mesosoma is entirely black and minutely imbricate, with scattered erect, white setae on the scutum, scutellum and pleura. The metasoma is entirely fuscous. Additional diagnostic features of males include the spatulate S8, and an unusual genital capsule. In lateral view the apex of the gonocoxite bears three prongs: one prong extends from the dorsal surface, and a pair of prongs extend from the ventral surface.

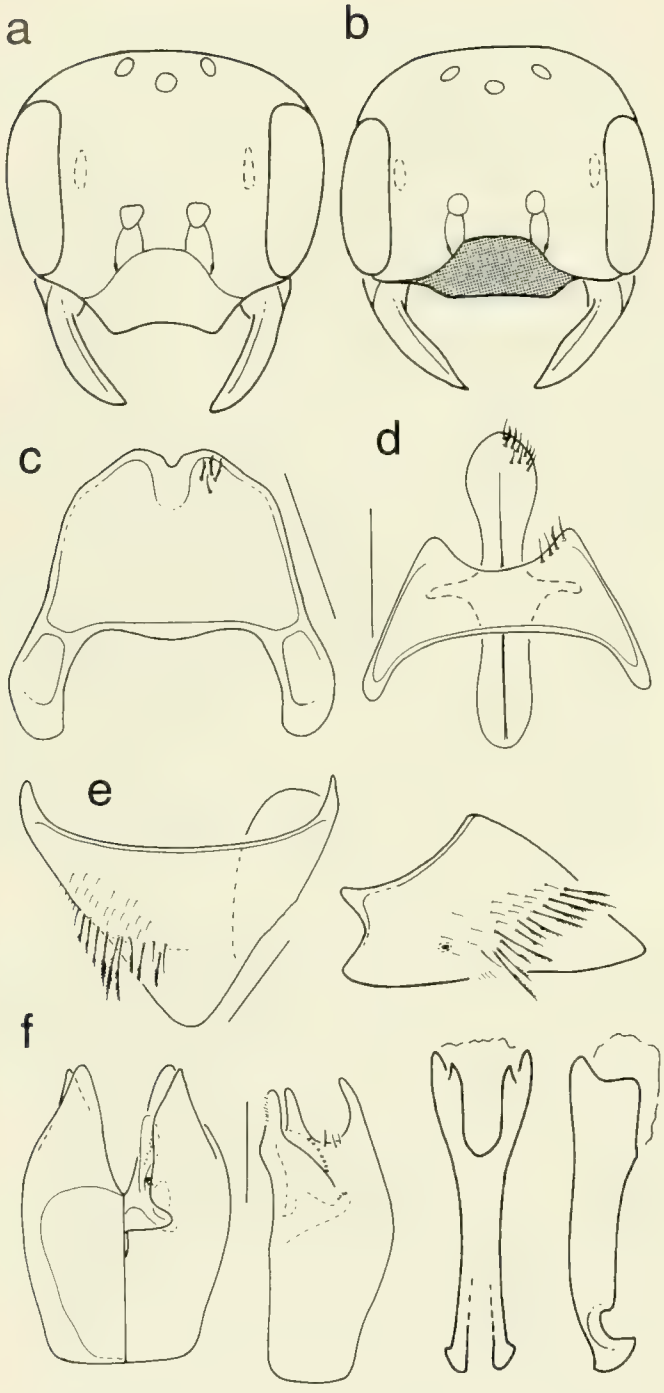


Fig. 29. *Perdita nigrella.* **(a)** female head, **(b)** male head, **(c)** female S6, **(d)** male S7 and S8, **(e)** male T7, dorsal and lateral views, **(f)** male genital capsule (dorsal, ventral and lateral views), aedeagus (dorsal and lateral view).

Distribution – Arid regions of Inyo county near Death Valley and Panamint Mountains, and desertic portions of Riverside county, California (Fig. 30).

Phenology – April to May.

Floral associations – *Phacelia* (*crenulata*) (7 females/3 males)

Perdita (*Macroterella*) *tristella* Timberlake

(Figs. 31, 35)

Perdita (*Macroterella*) *tristella* Timberlake, 1954: 363 [description]; 1954:361 [key]; 1968:7 [key].

Type material – The holotype male and allotype are in the CAS (Type No. 14741). Both specimens were collected at The Gavilan, Riverside Co., California, May 8 and 12, 1950, on *Eriogonum fasciculatum,* (Timberlake, coll.).

Diagnosis – Forewing length 2.4 - 2.6 mm. Females are all black with scattered erect white setae over the frons, mesoscutum, scutellum, pleura, metanotum and lateral surfaces of propodeum. The female head is 1.1 times broader than long, the frons has a blue-green, metallic tinge, and the facial foveae are large and broad, and lined with minute setae. The basitibial plates are very clearly defined on all sides (more so than in any other black *Macroterella*), triangular, and covered with a few short, recumbent finely branched setae. The female is unique in the shape of S6: the apicial margin has a slender slit flanked on either side by erect, finely branched setae. This feature can be seen without dissecting the apical segments. The male is similar to *P. nigrella* but can be distinguished by the shape of the S7, the genital capsule, and a modified S1: the posterior margin is reflexed medially into an acute protuberance which projects above the plane of S2 (this feature is not considered homologous to the modified S1 seen in some *Cockerellula*).

Distribution – Cismontane regions of Riverside Co., California (Fig. 35).

Phenology – April through June.

Floral associations – Although collected on *Eriastrum virgata* (1 female), *Calochortus splendens* (1 female), and *Sphaeralcea ambigua* (1 female), *Eriogonum* (*fasciculatum*) (1 female/5 males) appears to be the source of pollen, based on inspection of pollen in the scopa of females (Timberlake, 1954:363).

Perdita (*Macroterella*) *carinata* Timberlake

(Figs. 32, 35)

Perdita (*Macroterella*) *carinata* Timberlake, 1968:9 [description]

Type material – The holotype male and allotype are in the CAS (Type No. 14453). Both specimens were collected at the Boyd Desert Research Center, Deep Canyon, Riverside Co., California, May 10, 1963, on *Eschscholtzia* (E.I. Schlinger, coll.).

Diagnosis – Forewing length 2.3 - 2.7 mm. Females are predominantly black with yellow on the anterior surface of the foretibia and mandibles. The head and thorax are minutely imbricate, giving the surface of the body a tesselate appearance. Males are lighter colored than females; the head is brownish ferruginous to black with yellow on the mandibles, labrum, clypeus and supraclypeal area. The pronotum is light brown and the rest of the mesosoma darker brown. The metasoma is ferruginous and the male T7 is tubular and bears a distinct median, longitudinal carina on the apical margin.

Distribution – Collected most frequently in the vicinity of Deep Canyon, Riverside county, but also occurs in the arid parts of San Bernardino and Imperial counties, California; Pima, Pinal counties, Arizona; Baja California Sur, Mexico (Fig. 35).

Phenology – April through May; August through October.

Floral associations – Collected most commonly on *Eschscholtzia* (7 females/12 males) and *Euphorbia* (*hirtella*) (6 females/7 males) but also on *Ferrocactus* (*acanthodes*) (2 females/3 males), *Eriogonum* (1 female), *Echinocactus* (2 males) and *Opuntia* (1 male).

Perdita carinata and the next two species (*P. mortuaria* and *P. opacella*) are similar to each other, sharing the following characters: (1) male T7 tubular, lateral margins nearly touching ventrally, (2) genital capsules similar in shape, (3) scutum and scutellum minutely imbricate, lacking erect setae and seemingly impunctate,

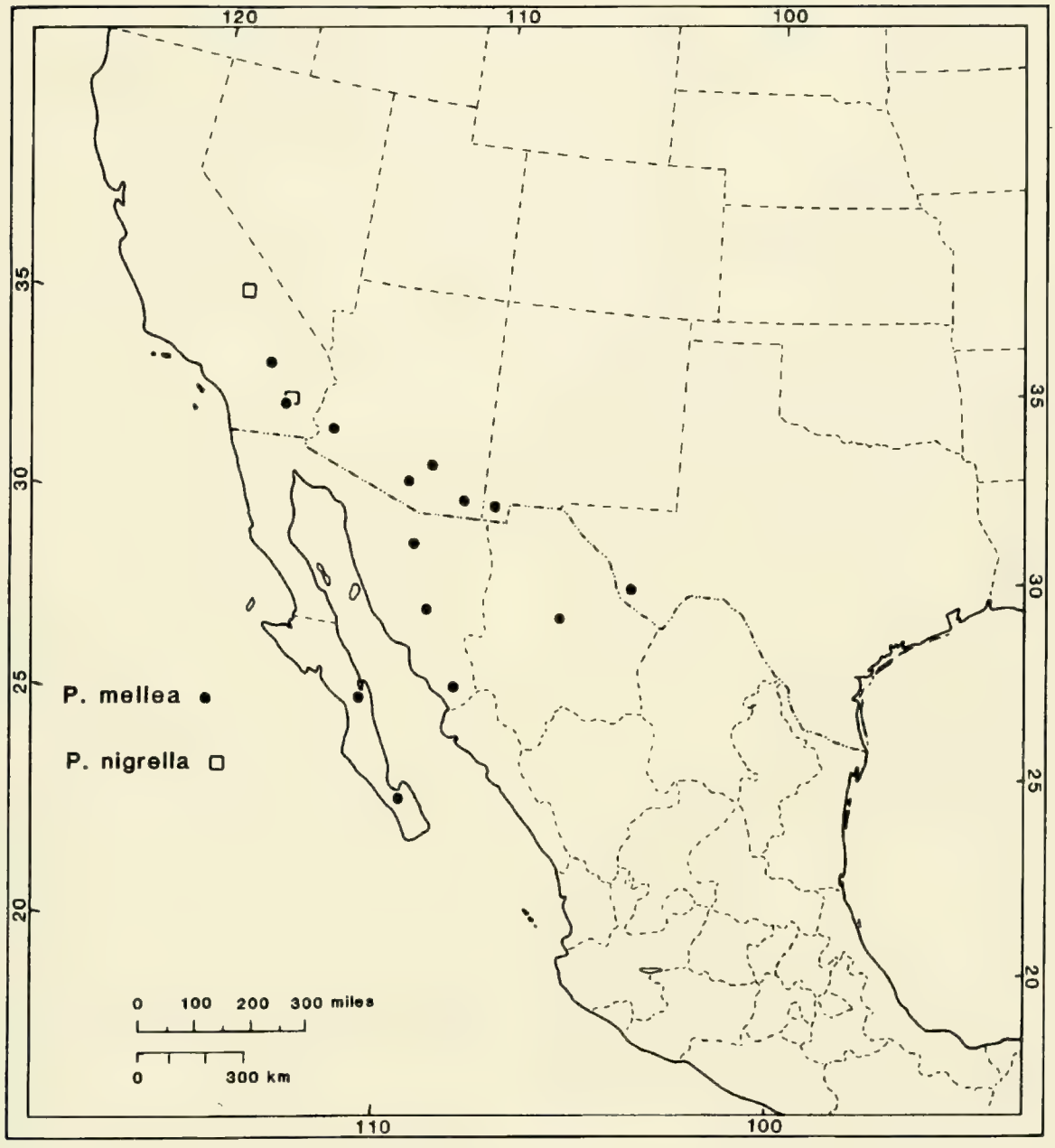


Fig. 30. Geographic distributions of *P. mellea* and *P. nigrella*.

however with a fine recumbent pubsecense visible under high magnification, and (4) anterior surfaces of foretibiae and mandibles yellowish in females. Females of these three species are extremely difficult to distinguish without associated males.

Perdita (*Macroterella*) *mortuaria* Timberlake

(Figs. 33, 35)

Perdita (*Macroterella*) *mortuaria* Timberlake, 1954:362 [description]; 1954:361 [key]; 1956:324 [additional material]; 1960:126 [additional material]; 1968:7-8 [key]; 1968:10 [additional material]; 1980:7 [new records].

Type material – The male holotype and allotype are located in the CAS (Type No. 14617). Both specimens were collected at Furnace Creek, Death Valley, Inyo Co., California, April 23, 1935, on *Eucnide urens* (A.L. Melander, coll.). The male holotype is missing the head.

Diagnosis – Forewing length 2.4-2.7 mm. The female is similar to *P. carinata*, but facial foveae are longer and parallel the eye margin (Timberlake, 1968:7). The male is similar to *P. carinata* in coloration and cuticular sculpturing. However, in *P. mortuaria*, although the male T7 is tubular, it lacks the longitudinal carina at the apex.

Distribution – Desertic and arid montane regions of Riverside, Inyo, Imperial counties, California; Maricopa, Yuma, Mojave, Co-

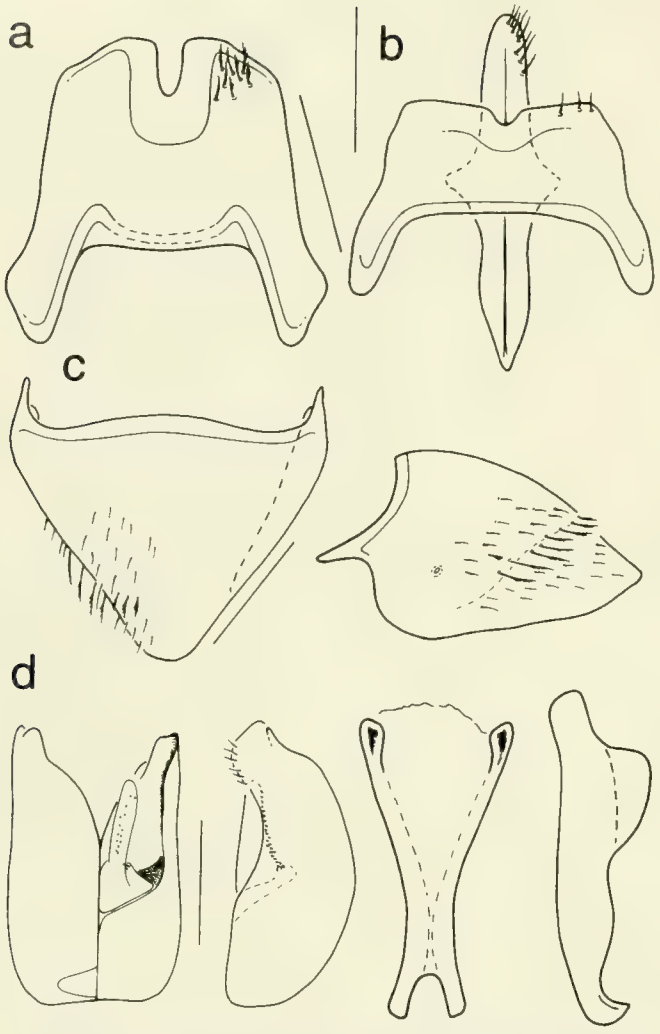


Fig. 31. *Perdita tristella.* **(a)** female head, **(b)** male head, **(c),** female S6, **(d)** male S7 and S8, **(e)** male T7, dorsal and lateral views, **(f)** male genital capsule (dorsal, ventral and lateral views), aedeagus (dorsal and lateral view).

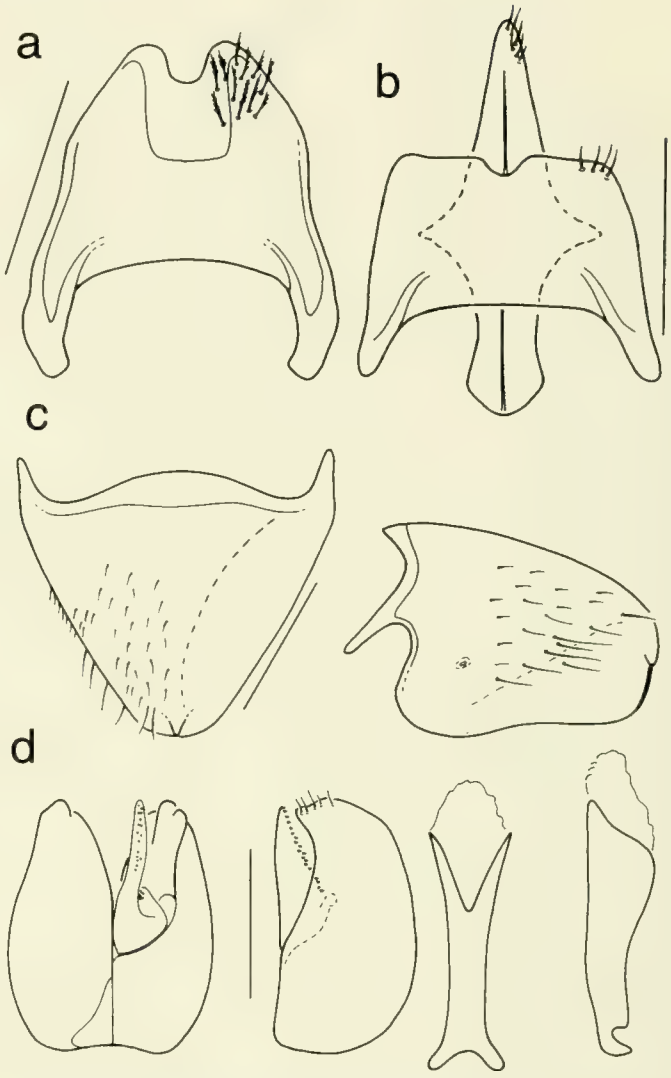


Fig. 32. *Perdita carinata.* **(a)** female S6, **(b)** male S7 and S8, **(c)** male T7, dorsal and lateral views, **(d)** male genital capsule (dorsal, ventral and lateral views), aedeagus (dorsal and lateral view).

conino, Cochise counties, Arizona; Hidalgo Co., New Mexico; Clark Co., Nevada (Fig. 35).

Phenology – March through June.

Floral associations – Collected most frequently on *Eschscholtzia* (*parishii, mexicana, darwinensis, minutiflora*) (10 females/6 males), which is seemingly the source of pollen, but also collected on *Prosopis* (4 females/1 male), *Eriogonum* (*inflatum, abertianum*) (2 females/1 male), *Eucnide urens* (5 males), *Larrea divaricata* (1 male), *Phacelia calthifolia* (1 female), *Echinocereus engelmanni* (1 female).

Perdita (*Macroterella*) *opacella* Timberlake

(Figs. 27c, 34, 35)

Perdita (*Macroterella*) *opacella* Timberlake, 1956:324 [description of female]; 1968:7,8 [key]; 1968:8 [description of male].

Type material – The female holotype is located in the CAS (Type No. 14644). This specimen was collected at Marble Canyon, near Lee's Ferry, Grand Canyon, Coconino Co., Arizona, June 5 1953, on *Stanleya* (G.D. Butler, coll.).

Diagnosis – Forewing length 2.5 - 2.8 mm. The female is similar to *P. carinata* and *P. mortuaria,* but can be distinguished from these two species by the shape of the pygidial plate (broader and more obtuse apically) and by the presence of faint metallic greenish tinge on the frons (Timberlake, 1968:8). Males are similar to the preceding two species in coloration and punctation; however, with more creamy-white facial maculation, which extends up to the level of the antennal sockets. Males are most easily distinguished from all other members of *Macroterella* by the shape of T7: dorsoapically it bears two lateroposteriorly directed protuberances which are separated along the posterior margin of the tergum by a deep median slit. As in the other two species, the lateral margins of T7 meet ventrally to form a tube through which the genitalia project, in some specimens. The genital capsule is distinctive as well.

Distribution – Desertic regions of Coconino and Cochise counties, Arizona; San Juan Co., Utah (Fig. 35).

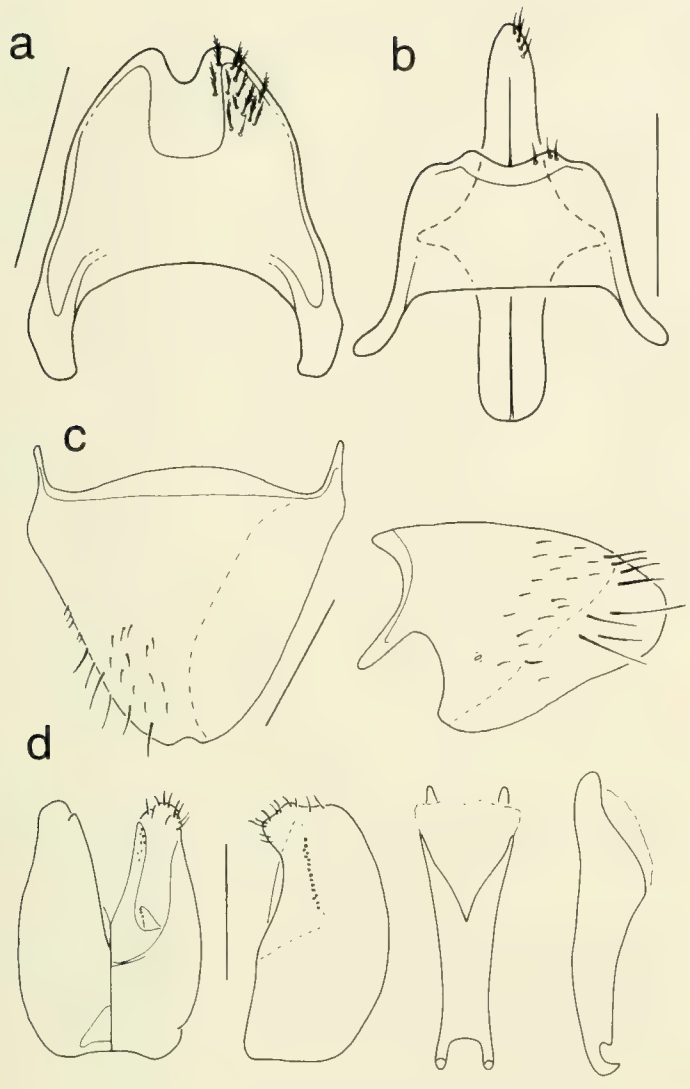


Fig. 33. *Perdita mortuaria.* **(a)** female S6, **(b)** male S7 and S8, **(c)** male T7, dorsal and lateral views, **(d)** male genital capsule (dorsal, ventral and lateral views), aedeagus (dorsal and lateral view).

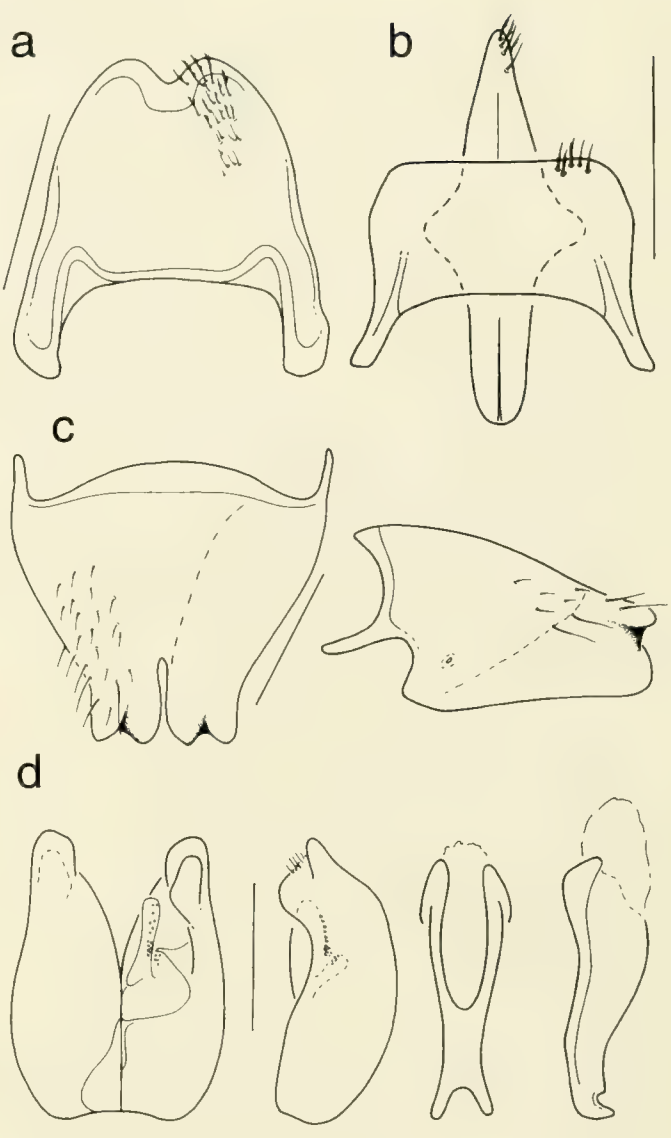


Fig. 34. *Perdita opacella.* **(a)** female S6, **(b)** male S7 and S8, **(c)** male T7, dorsal and lateral views, **(d)** male genital capsule (dorsal, ventral and lateral views), aedeagus (dorsal and lateral view).

Phenology – June and August.

Floral associations– *Cleome lutea* (7 females/11 males) is almost certainly the primary source of pollen for this species, although females have been collected on *Stanleya* (1 female) and *Eriogonum abertianum neomexicanum* (1 female).

Subgenus *Macrotera* Smith

Macrotera Smith, 1853:130 [description]; Cresson, 1878:70-71 [additional species]; Cockerell, 1904 [additional species]; Cockerell, 1905; Timberlake, 1954:352 [diagnosis and key to species]; 1958:375-378 [additional species and key to species]; Snelling & Danforth, 1992 [additional species, keys to species].

Type species – *Perdita bicolor* Smith, monobasic.

Diagnosis – The species in this subgenus are distinguished by: (1) large body size (forewing length usually exceeding 4.5 mm and often approaching 5.0 mm); (2) glossa two or more, usually three, times length of prementum (Fig. 27d); (3) male with pygidial plate on T7; (4) second maxillary palpal segment longer than first, or any other segments.

All the species in this subgenus are oligolectic on *Opuntia.* Females of this subgenus are very hard to identify to species without associated males. The female S6 is the most useful structure for distinguishing females of this group. The subgenus ranges from Oklahoma and northern Texas (*P. crassa* and *P. texana*) to southern Mexico (*P. bicolor*).

Snelling and Danforth (1992) published taxonomic notes, keys, and illustrations of *Macrotera.*

Subgenus *Macroteropsis* Ashmead

Macroteropsis Ashmead, 1899:85; Cockerell & Porter, 1899:417 [de-

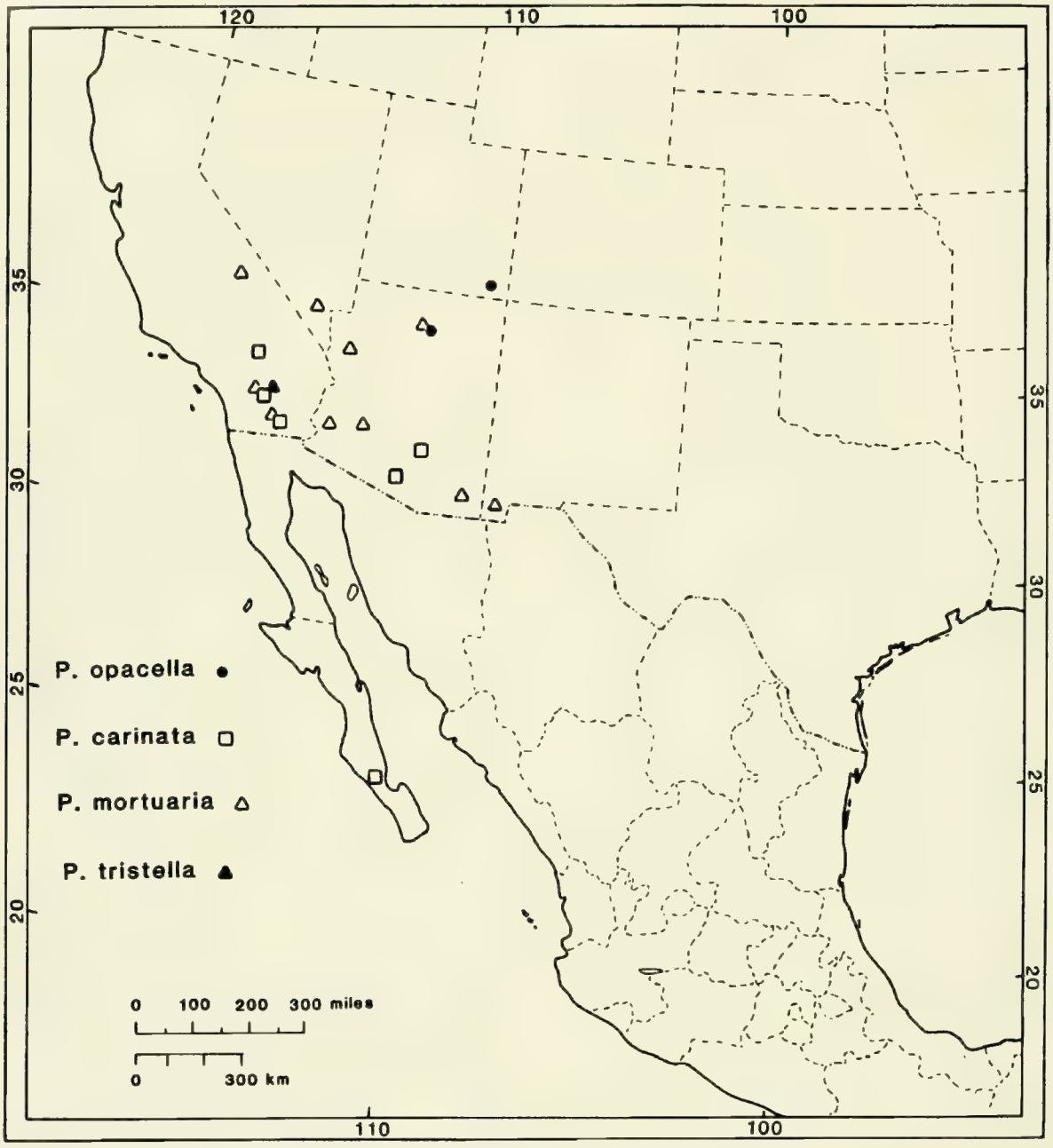


Fig. 35. Geographic distributions of *P. opacella, P. carinata, P. mortuaria, P. tristella.*

scription]; Timberlake 1954:356-360 [description, key to species]; 1956:323 [additional material; 1960:124 [additional material]; 1962:87-89 [key to males, additional material]; 1968:4-7 [additional species]; 1980:2-5 [key to females, additional species].

Type species – *Perdita latior* Cockerell, by original designation.

Diagnosis – This subgenus is easily recognized based on the following characters: (1) second labial palpus arising subapically on first, and first tapering to an acute point (Fig. 36 a,b), (2) maxillary palpal segments, especially distal segments, reduced in length and obscure or totally absent (in most species the number of maxillary palpal segments is reduced from 6 to 5 or 4), (3) head of female relatively broad (maximum width roughly 1.3 times the length from vertex to clypeal margin), and eyes protuberant, (4) females with dense, erect, finely branched white setae over head and mesonotum, (5) female metasoma dark brown to black, usually lacking any reddish coloration, (6) metallic sheen on frons and mesosoma.

***Perdita (Macroteropsis) arcuata* Fox**

(Figs. 37, 41)

Perdita arcuata Fox, 1893:18 [description of male]; Cockerell, 1896:54.

Perdita dinognatha Cockerell 1922a:19 [description of male].

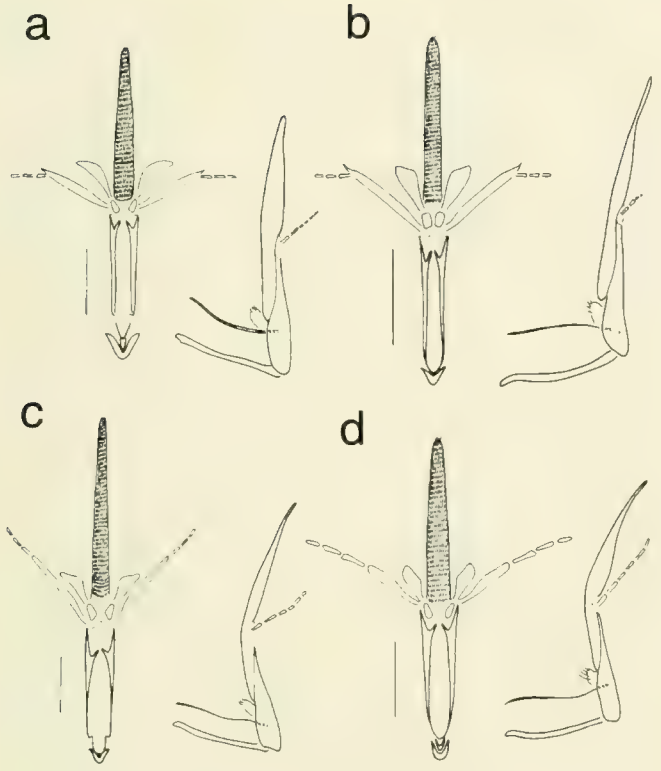


Fig. 36. Mouthpart morphology, females. **(a)** *P. echinocacti*, **(b)** *P. portalis*, **(c)** *P. azteca*, **(d)** *P. solitaria* (Scale bar = 0.5 mm).

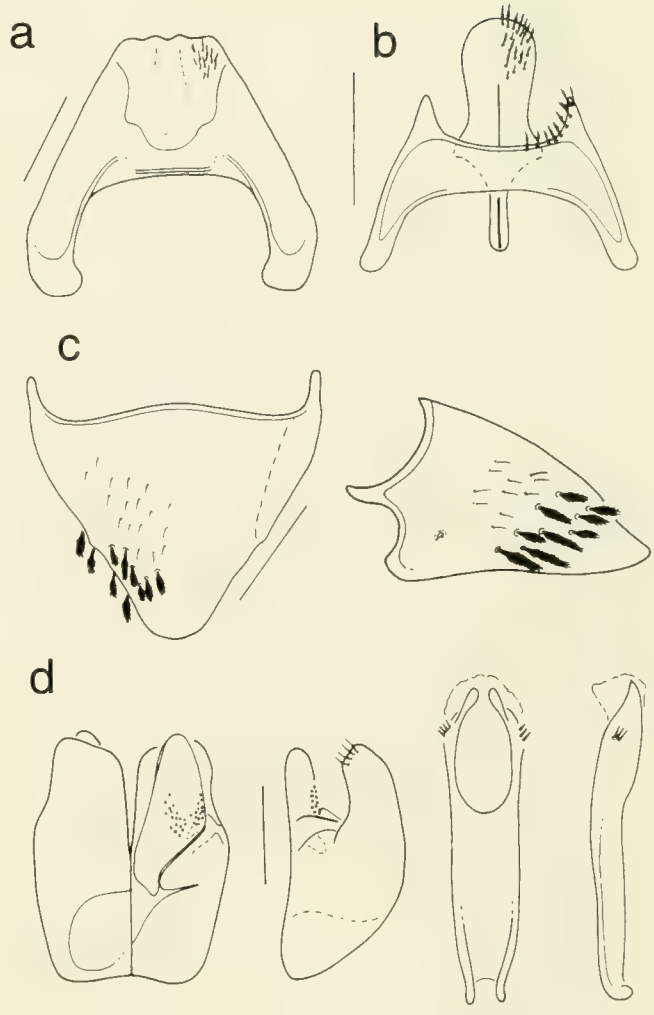


Fig. 37. *Perdita arcuata*. **(a)** female S6, **(b)** male S7 and S8, **(c)** male T7, dorsal and lateral views, **(d)** male genital capsule (dorsal, ventral and lateral views), aedeagus (dorsal and lateral view).

Perdita (*Macroteropsis*) *arcuata arcuata:* Timberlake, 1953:968; 1954:358 [new localities]; 1954:357 [key]; 1962:87 [key]; 1968:4 [additional material and comments on distribution]; 1980:3 [key]. *Perdita* (*Macropteropsis*) *arcuata dinognatha:* Timberlake 1953:968 [additional material]; Timberlake, 1954:359 [description of female and additional material]; 1980:3 [key].

Type material – The male lectotype (Type No. 275) and the allotype (Type No. 276) are located in the CAS. The lectotype was collected at Calmalli Mines, Baja California Norte, Mexico (Fox, coll.). The male holotype of *P. dinognatha* is located in the NMNH (Cat. No. 24895) and was collected at San Diego Co., California, April (Coquillett, coll.).

Diagnosis – Forewing length 3.0 - 4.0 mm. Males of this species can be distinguished from all other species of *Macroteropsis* by the simple mandibles, lacking a pollex, and by the quadrate labrum with a transverse ridge across the middle (all other species have a round or ovoid labrum lacking a transverse ridge). Females have a uniquely-shaped S6 with the central pale area broad (length only 2-3 times width) while in *P. echinocacti* and *P. latior* the central pale area is very slender (length 5-6 times width). This is the best character for positively identifying females.

The two previously recognized subspecies of *P. arcuata* are not recognized here because no consistent suite of congruent characters could be found to delineate them. The two characters on which the distinction was based were the presence/absence of yellow maculation on the male clypeus and the number of maxillary palpal segments (5 or 6). The majority of the male specimens from Baja California lack yellow maculation on the clypeus (Timberlake, 1953:968) and most (10/12; 7 males, 5 females) of the specimens I dissected had 6-segmented maxillary palpi. In constrast, all 22 (16 males, 6 females) of the specimens from the states of Arizona and California had 5-segmented palpi and most of these males had yellow maculation on the clypeus. However, the specimens from San Benito Co., California, present somewhat of a problem. They possess both the derived traits of lacking yellow maculation and of reduced maxillary palpi. Timberlake (1968:4) considered them to belong to the subspecies *arcuata* because of the former character, and concluded that the true range of *P.* (*a.*) *arcuata* was coastal California from San Benito Co. to Baja California Sur. However, 5-segmented maxillary palpi suggest that this population is more closely related to the other California (and Arizona) populations than to those in Baja California.

Description – FEMALE – Head: (1) width 1.52-1.88 mm (x = 1.69 ± 0.05; n=6); (2) 1.3-1.4 times broader than long (as measured from the vertex to the lower margin of the clypeus); (3) clypeus weakly imbricate-punctate; (4) frons granulate with small punctures and with linear depression along midline; (5) vertex imbricate-punctate; (6) gena imbricate with scattered punctures; (7) head coloration dark brown with metallic blue or green sheen, strongest on the frons; (8) whole head clothed in white, finely-branched setae, recumbent and shorter on clypeus and frons, erect and longest

on vertex and genae; (9) inner margins of eyes diverging very slightly above; eyes brownish; (10) posterior ocelli at level of upper margin of compound eye; (11) facial foveae deeply impressed, elongate and broadened slightly dorsally; (12) scape of antenna equal in length to flagellar segments 1-6, first flagellar segment slightly longer than second.

Mouthparts: (13) labrum with central depressed area, clothed with erect, finely-branched setae, and central transverse ridge; (14) mandible rufous, bidentate, with sulcus originating at mandibular acetabulum and extending diagonally across base of mandible; (15) glossa elongate, roughly 1.25 times longer than prementum; (16) paraglossa slender basally but expanding distally into broad, brushlike apex; (17) labial palpus 4-segmented, first segment longer than remaining segments combined and second segment inserted subapically on first; (18) galeal comb absent or present and very small; (19) maxillary palpus 5-6 segmented, distal segments (3 to end) greatly shortened so that overall length of palpus short.

Mesosoma: (20) pronotum brownish with transverse sulcus dorsally and fringe of erect setae on leading edge; dorsal surface glabrous and with scattered punctures becoming imbricate laterally; pronotal lobe with coarsely branched setae; (21) mesoscutum black with metallic blue sheen; surface minutely imbricate-punctate with two types of setae: small recumbent setae and more widely scattered elongate erect setae; notauli (weak), parapsidal lines and central longitudinal sulcus present; (22) mesoscutellum and metanotum brownish with similar sculpturing and setae; (23) mesopleuron brown with faint metallic blue or green sheen; sculpturing imbricate-punctate anterior to scrobe, reticulate posterior to scrobe; scrobal sulcus absent; (24) metapleuron reticulate, lacking setae; (25) propodeum reticulate dorsally, becoming glabrous posteriorly; paired patches of erect setae flank central glabrous area; laterally, below spiracle, cuticle imbricate; (26) intertegular distance 1.12 - 1.18 mm ($x = 1.16 \pm 0.01$; n=6); (27) forewing length 3.16 - 4.00 mm ($x = 3.75 \pm 0.12$; n=6); wings slightly opaque with brownish tinge, veins brown; (28) legs brown; forecoxa with long, erect, unbranched, posterior-directed setae; (29) basitibial plate distinct, the cental portion clothed in recumbent setae; (30) scopal hairs on anterior surface of tibia simple, becoming finely branched along outer edge of tibia; (31) midtibial spur finely serrate and gently hooked at apex; (32) hind tibial spurs subequal in length (inner slightly longer than outer) and finely serrate; (33) tarsal claws all bifid.

Metasoma: (34) terga dark brown, with paler transparent apical margin; (35) terga 1-5 minutely imbricate-punctate with small posteriorly-directed, recumbent setae; on cleared terga pale membranous slits extend from leading edge to spiracle; (36) deeply impressed fovea on lateral edge of T2; (37) T5 with long, erect, plumose setae along posterior margin; (38) graduli on T2-T4; (39) T6 with raised, acutely pointed pygidial plate flanked by dense, plumose setae; central portion of pygidial plate colliculate; (40) sterna slightly paler than terga; sterna 1-5 similar in sculpturing and vestiture to terga; (41) S6 as in Fig. 37a; (42) sternal graduli lacking on all segments except S1, where they are present only laterally.

MALE – Head: (43) width 1.20 - 1.96 mm ($x = 1.57 \pm 0.08$; n=8); (44) quadrate, 1.4 - 1.6 times broader than long; (45) clypeus broad and dorso-ventrally compressed, surface weakly imbricate-punctate; (46) frons granulate with many small punctures and with median linear depression above level of antennal sockets; (47) vertex imbricate-punctate; (48) gena imbricate-punctate; (49) head deep brown, becoming paler at clypeus which may be yellow in specimens from California (except San Benito Co.), Arizona and Nevada; blue or olive metallic sheen becoming strongest on frons; (50) head clothed in finely-branched setae, recumbent on clypeus and supraclypeal area, erect and longer on upper part of frons, vertex and genae; (51) inner margins of eyes subparallel; (52) posterior ocelli just above level of upper margin of compound eyes; (53) facial fovea weakly impressed, oval or teardrop shaped; (54) antennae brown.

Mouthparts: (55) labrum pale brown to yellow, rectangular, broader than long, with transverse ridge and scattered, finely-branched setae; (56) mandible yellow, with reddish tips; no subapical tooth and with outer sulcus (as in female); (57-61) male mouthparts as in female except paraglossae slender and acutely pointed, not broad and brushlike.

Mesosoma: (62-67) coloration and sculpturing of mesosoma as in female; (68) intertegular distance 0.92 - 1.24 ($x = 1.08 \pm 0.04$, n=8); (69) forewing length 2.84 - 3.72 ($x = 3.33 \pm 0.12$; n=8); wings as in female except for veins forming the posterior and distal margins of second medial cell (veins Cu1a and 2m-cu), which are distinctly weaker than other veins; (70) legs brown, or in some specimens, with yellow maculation on inner surface of fore-tibia; (71) basitibial plate concave and well defined around entire margin; surface of plate with a few apressed setae; (72) outer surface of hind tibia imbricate with stout moss-like setae; (73-75) tibial spurs and tarsal claws as in female.

Metasoma: (76) terga brown to reddish brown; (77) terga 1-6 minutely punctate with small, recumbent, white setae; (78) single row of stout moss-like setae across T6; (79) faint longitudinal fovea on lateral edge of T2; (80) T7 with paired patches of moss-like setae apically; lacking pygidial plate; anterior edge convex in dorsal view; (81) graduli present on terga 2-6; weak lateral extensions of graduli on T2 and T3; (82) sterna similar in coloration to terga; (83) sterna 1-6 similar in vestiture and coloration to terga 1-6; (84) sternal graduli present laterally on S1 and complete on S2-S5; (85) S7 and S8 as in Fig. 37b; (86) genital capsule with broad, horizontal gonocoxites clothed apically with setae; (87) volsellar cuspis large with papillae located dorsally sometimes restricted to base of cuspis and sometimes extending to the apex; (88) digitus with papillae; (89) penis valves with two patches of stout setae laterally (Fig. 37d).

Distribution – Throughout desertic and montane regions of Riverside, San Bernardino, Inyo, San Diego, Imperial, San Benito counties, California; Mojave, Yavapai, Coconino, Yuma, Pima, Maricopa counties, Arizona; Clark Co., Nevada; Washington, San Juan counties, Utah; Baja California Norte and Sur, Mexico (Fig. 41).

Phenology – April through July, and October (in Baja California).

Floral associations – Collected primarily on *Sphaeralcea* (*ambigua, rosacea*) (224 females/340 males); but also collected on *Hibiscus denudatus* (1 female), *Malva* (2 males), *Eriogonum polyfolium* (1 female), *Eriodictyon trichocalyx* (1 male), *Echinocactus acanthodes* (1 female), *Eschscholtzia californica* (1 male), *Malacothamnus orbiculatus* (1 male), *Encelia frutescens* (1 male/1 female), *Hemizonia lobbii* (1 male).

Perdita (*Macroteropsis*) *echinocacti* Timberlake

(Figs. 36a, 38, 41)

Perdita (*Macroteropsis*) *echinocacti* Timberlake, 1954:360 [description]; 1954:357 [key]; 1960:125 [additional material]; 1962:87 [key]; 1980:3 [key]; Simpson & Neff, 1987:426 [biology].

Perdita tepicensis Timberlake, 1968:5 [description of male] NEW SYNONYMY.

Type material – The holotype male and allotype are in the CAS (Type No. 14499). The type specimens were collected 4 1/2 miles

above Pepper Sauce Canyon, Santa Catalina Mts., Pima Co., Arizona, August 14, 1940, on *Echinocactus* (Timberlake, coll.). The holotype male of *P. tepicensis* is at KU, and was collected west of Tepic, Nayarit, Mexico, 1600 ft., Aug. 19, 1961 (C.F. Bennett, coll.).

Diagnosis – Forewing length 3.0 - 3.7 mm. Males have yellow maculation on the labrum, clypeus and supraclypeal area up to the level of the antennal sockets, and have a bluish metallic sheen on the frons and mesonotum. Unlike males of the other members of *Macroteropsis* (except *P. latior*), males of this species have a pygidial plate on T7 formed by two parallel carinae. The presence of a median, posteriorly-directed prong on male S2 will distinguish this species from all other *Macroteropsis*. In both males and females the maxillary palpi are distinctly 6-segmented; segments 1 and 2 are subequal and relatively long; segments 3-6 are much shorter. Females can be distinguished from other *Macroteropsis* (except *P. latior*) by the shape of S6 (central clear area 5-6 times longer than wide), by the maxillary palpi, and by the distinctly bluish tinge to the frons and mesonotum.

I see no reason to consider the holotype of *P. tepicensis* distinct from *P. echinocacti*. According to Timberlake this species differs from the former in the sculpturing of the mesonotum. However, the seemingly unique cuticular sculpturing of the *P. tepicensis* holotype results from dirt caked on the specimen.

Distribution – Pinal, Pima, Santa Cruz, Cochise counties, Arizona; states of Sonora, Sinaloa and south to Nayarit (the type locality of *P. tepicensis*), Mexico (Fig. 41). Additional specimens are recorded from Chihuahua, Mexico by PCAM (Ayala, et al., 1996), but I have not examined these specimens myself.

Phenology – August through September.

Floral associations – *Kallstroemia* (*grandiflora*) (44 females/54 males), *Echinocactus* (*wislezeni* [sic]) (12 females/36 males), *Convolvulus* (6 females/16 males), *Antigonum* (3 females), *Boerhaavia* (1 female/1 male), *Ferocactus* (1 female/2 males). Although this species is commonly thought to be a cactus oligolege, the frequency of females on *Kallstroemia* suggests this as a possible pollen source as well.

Perdita (*Macroteropsis*) *latior* Cockerell

(Figs. 39, 41)

Perdita latior Cockerell, 1896:53 [description]; Cockerell, 1897a:354 [flower record].

Macroteropsis latior: Cockerell and Porter, 1899:417.

Perdita (*Macroteropsis*) *latior:* Timberlake, 1953:968 [additional material]; Timberlake, 1954:359 [localities and flower records]; 1954:357 [key]; 1962:87 [key]; 1980:3 [key].

Type material – One female co-type is located in the USNM (Type No. 3365). This specimen was collected at Las Cruces, Dona Ana Co., New Mexico, August 1895, on *Sphaeralcea angustifolia* (Cockerell, coll.). Two additional co-types are located at the Academy of Natural Sciences of Philadelphia. Both specimens were collected at the same locality as the co-type in the USNM. Along with the locality and host plant labels, the male bears the label "Ckll. 4815" and the female bears the label "Ckll. 4822." I designate the male at the Academy of Natural Sciences the lectotype.

Diagnosis – Forewing length 2.9 - 4.0 mm. *P. latior* is very similar to *P. echinocacti*. The males can be distinguished from *P. echinocacti* because they lack the prong on the apical margin of S2. The yellow facial maculation is less extensive on the face of *P. latior*, scarcely reaching the upper margin of the clypeus laterally, whereas in *P. echinocacti* the yellow extends upward along the inner margins of the eyes to above the level of the antennal sockets. Maxillary palpi are 6-segmented, as in *P. echinocacti*, but segment 5 is often indistinct. Females of these two species are difficult to distinguish (Timberlake, 1954:360) and it is best to rely on associated males. However, in the absence of males, this species may be distinguished from *P. echinocacti* by (1) the more bluish tinge on frons and mesoscutum in *P. echinocacti*, and (2) the more elongate and slender central pale area on the female S6 in *P. latior*, as compared to *P. echinocacti*.

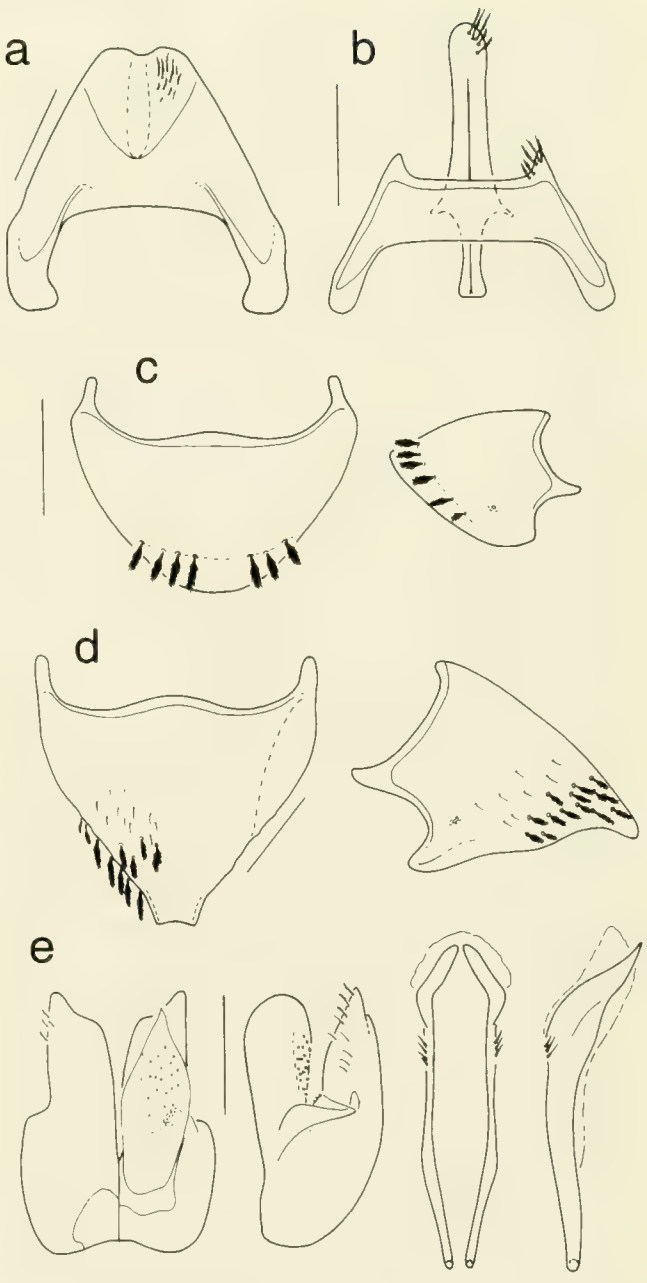


Fig. 38. *Perdita echinocacti.* **(a)** female S6, **(b)** male S7 and S8, **(c)** male T6, dorsal and lateral views showing moss-like setae along posterior margin, **(d)** male T7, dorsal and lateral views, **(e)** male genital capsule (dorsal, ventral and lateral views), aedeagus (dorsal and lateral view).

Distribution – Desertic regions of Cochise, Yavapai, Coconino, Apache, Navajo, Gila, Mojave, Pima, Pinal counties Arizona; Dona Ana, Sandoval, Santa Fe, Hidalgo, Grant, Valencia, McKinley, Lin-

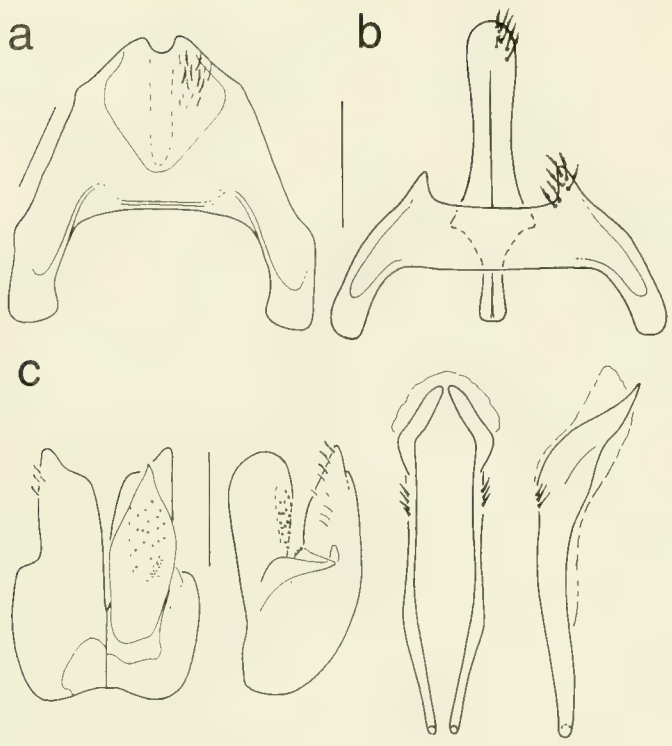


Fig. 39. *Perdita latior.* **(a)** female S6, **(b)** male S7 and S8, **(c)** male genital capsule (dorsal, ventral and lateral views), aedeagus (dorsal and lateral view).

coln counties New Mexico; Robertson Co., Texas; Clark Co., Nevada; Sonora, Mexico (Fig. 41). Additional specimens are recorded from Chihuahua, Mexico by PCAM (Ayala, et al., 1996), but I have not examined these specimens myself.

Phenology – May through October.

Floral associations – The vast majority of specimens were collected on *Sphaeralcea* (*angustifolia*) (115 females/108 males) and this is apparently the sole pollen source, but specimens have also been collected on *Heterotheca subaxillaris* (5 females), *Malva* (1 male), *Sida heteracea* [sic] (1 female), *Tidestromia lanuginosa* (1 male), *Helenium hoopesi* (1 female) and *Lygodesmia juncea* (1 female).

Perdita (*Macroteropsis*) *magniceps* Timberlake

(Figs. 40, 41)

Perdita (*Macroteropsis*) *magniceps* Timberlake, 1960:124 [description of male].

Type material – The male holotype is located in the CAS (Type No. 14597). The holotype was collected 17 miles east of Deming, Luna Co., New Mexico, September 13, 1957, on *Kallstroemia* (Timberlake, coll.).

Diagnosis – Forewing length 3.2 - 3.8 mm. At the time Timberlake described this species there was only a single, rather large-headed, male specimen available. Since his original description was written, a long series of both male and female specimens have been collected at several additional localities and a more complete description of male variation can be given along with a description of the female (see below). The male of this species is clearly distinct from all other species of the subgenus *Macroteropsis*. In all specimens the head is orange-ferruginous with small, black facial foveae. In the largest specimens (head width = 1.6 mm) the head is almost entirely glabrous except for sparsely distributed, small, appressed hairs over the frons and genae and a band of erect setae running across the vertex posterior to the ocelli. In lateral view, the gena of the largest males is expanded to 1.9 times the width of the compound eye, while the smallest specimens show almost no genal enlargement. Unlike in all other members of *Macroteropsis* there can be extensive orange-ferruginous maculation over the mesosoma. The extent of the maculation covaries with overall body size. In the smallest specimens orange-ferruginus maculations are restricted to the pronotum and a small central spot on the scutellum. In the largest specimens orange maculation covers the pronotum, the lateral portions of the mesopleuron, metapleuron and the entire propodeum, although the dorsal and posterior surfaces of the propodeum appear brownish. Dorsally, small lateral portions of the scutum, immediately above the forewing bases, the central parts of the scutellum and the mesono-

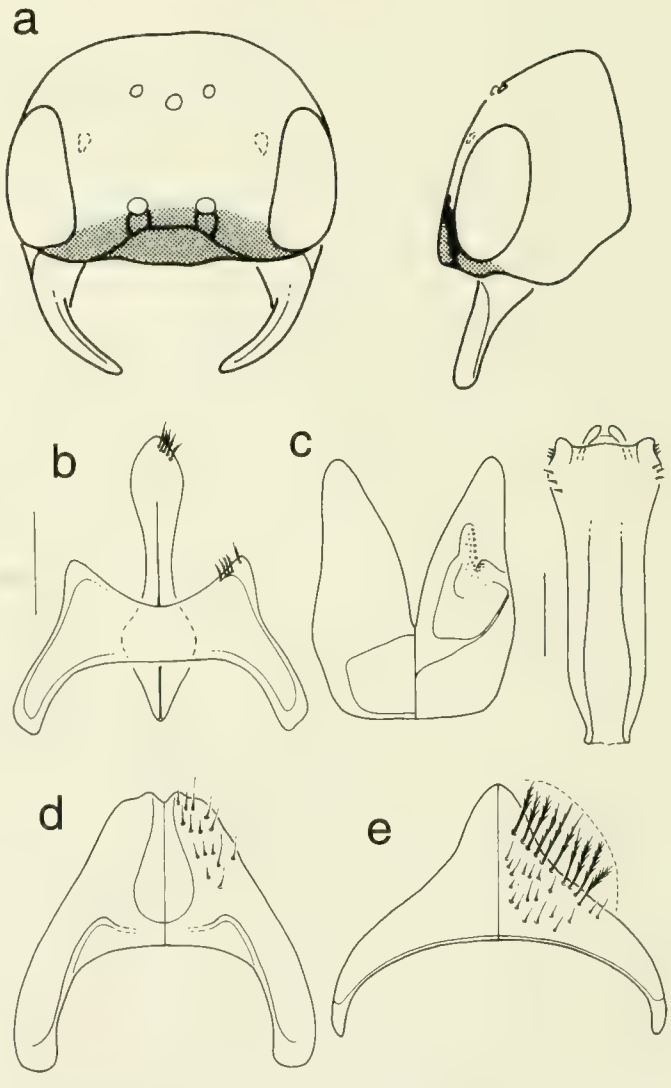


Fig. 40. *Perdita magniceps.* **(a)** male head, frontal and lateral views, **(b)** male S7 and S8, **(c)** male genital capsule (dorsal, ventral and lateral views), aedeagus (dorsal and lateral view), **(d)** female S6, **(e)** female T6.

tum are orange-ferruginous. The maxillary palpi are four-segmented, but unlike those of *P. haplura* and *P. portalis*, the mandibles are simple. The genital capsule, S7 and S8 slide mounted by Timberlake (slide no. 887) agree in all respects with the new material of this species, and serve to further distinguish this species from all other *Macroteropsis*.

Females are distinctive in showing similarly colored, although much less extensively distributed, orange-ferruginous maculation on the head and, in some specimens, the lateral lobes of the pronotum. Orange-ferruginous maculation is present on the mandibles, labrum, and clypeus, and extends upward as two thin bands on either side of the eye which meet dorsally and form a broad band along the vertex. The orange band extends medially from the eye and reaches the lateral ocellus in all specimens. The presence of orange-ferruginous bands on the vertex will separate this species from all others treated herein.

One of the most distinctive feature of this species, in both the males and females, is the extensive development of dense, closely appressed setae clothing the mesoscutum, scutellum and lateral portions of the mesopleura. These setae gives the females in particular a frosted appearance.

This species is united with *P. lation, P. echinocacti* and *P. arcuata* by the setae on the lateral surfaces of the penis valves.

Description – FEMALE – Head: (1) width 1.35 - 1.60 mm (x = 1.51 ± 0.20; n=10); (2) 1.30 - 1.40 (x = 1.34 ± 0.01; n=10) times broader than long (as measured from the vertex to the lower margin of the clypeus); (3) clypeus distinctly and densely punctate, with weakly imbricate regions between the punctation; (4) frons imbricate with small punctures and with linear depression along midline; (5) vertex imbricate with scattered punctations; (6) gena imbricate with scattered punctures; (7) head coloration primarily black with coppery sheen on frons and orange-ferruginous maculation with the following distribution: clypeus (along lower margin or extending upward to cover entire surface), in some specimens, small medial area between the antennal bases, thin band surrounding compound eyes and extending medially from upper margins of the compound eyes along vertex to lateral ocellus (never meeting to form continuous band across vertex); (8) entire face up to level of compound eyes clothed in closely appressed thick white setae in unworn specimens; more elongate, erect setae along vertex, lateral, and posterior portions of head; (9) inner margins of eyes diverging above; eyes brownish (in pinned specimens); (10) posterior ocelli at level of upper margin of compound eye; (11) facial foveae weakly impressed, slender (0.32 mm in length); difficult to see through hairs on unworn specimens; (12) scape of antenna equal in length to flagellar segments 1-5, first flagellar segment slightly longer than second.

Mouthparts: (13) labrum with central depressed area, clothed with erect, finely-branched setae, and central transverse ridge; (14) mandible yellow, becoming reddish apically; bidentate, with sulcus originating at mandibular acetabulum and extending diagonally across base of mandible; (15) glossa elongate and slender, roughly equal to prementum in length; (16) paraglossa slender basally but expanding distally into broad, brushlike apex; (17) labial palpus 4-segmented, first segment longer than remaining segments combined and second segment inserted subapically on first; (18) galeal comb absent or present and very small; (19) maxillary palpus 4-5 segmented at most, distal segments (3 to end) greatly shortened so that overall length of palpus short.

Mesosoma: (20) pronotum blackish with orange-ferruginous maculation weakly developed on lateral lobes and dorsal surface; dorsal and lateral surfaces imbricate and hairless; (21) mesoscutum black with metallic green or coppery sheen; surface coarsely imbricate-punctate with extremely dense clothing of white recument setae and more widely scattered longer, erect setae; notauli (weak), parapsidal lines and central longitudinal sulcus present; (22) mesoscutellum and metanotum dark brownish with similar sculpturing and setae but with more erect than recumbent setae; (23) mesopleuron weakly metallic; sculpturing reticulate-punctate dorsally becoming imbricate-punctate ventrally; setae on lateral portions of mesopleuron erect, white, and finely branched; setae on ventral portion of mesopleuron simple, distinct from ones on lateral portion; scrobal sulcus absent; (24) metapleuron reticulate, lacking setae; (25) propodeum imbricate to reticulate laterally; posterior surface glabrous; dorsal surface (propodeal triangle) with metallic bluish sheen and weakly imbricate; lateral and posterior surfaces separated by dense row of erect, white setae similar to those on metanotum and scutellum; (26) intertegular distance 1.12 - 1.28 mm (x = 1.18 ± 0.017; n=10); (27) forewing length 3.20 - 3.80 mm (x = 3.46 ± 0.04; n=10); wings milky white with pale yellowish to whitish wing veins; (28) legs mostly brown but apices of forefemur, most of foretibia, apices of mesofemur, base of mesotibia and apex of metafemur orange to fuscous; (29) basitibial plate quadrate and well-developed, with a few recumbent setae on its concave surface; (30) scopal hairs on anterior surface of tibia simple, becoming finely branched along outer edge of tibia; (31) midtibial spur finely serrate and very slightly hooked at apex; (32) hind tibial spurs finely serrate; subequal in length; (33) tarsal claws all bifid.

Metasoma: (34) most terga dark brown, with paler transparent apical margin; sometimes with weakly-defined light brown areas on anterior and dorsal surface of T1 and dorsal surface of T2; (35) terga 1-5 minutely imbricate-punctate with small posteriorly-directed, recumbent setae; pale membranous slits extending from leading edge to spiracle visible in cleared terga; (36) deeply impressed fovea on lateral edge of T2; (37) T5 with long, erect, plumose setae along posterior margin; (38) graduli on T2-T4; (39) T6 with raised, acutely pointed pygidial plate flanked by dense, plumose setae; central portion of pygidial plate colliculate; (40) sterna dark brown like terga; S1-S5 similar in sculpturing and vestiture to terga; (41) S6 as in *P. arcuata* (Fig. 40d); (42) sternal graduli lacking on all segments except S1, where they are present only laterally.

Distribution – Luna and Socorro counties, New Mexico; northern part of Chihuahua, Mexico (Fig. 41). This species seems to be restricted to mostly sandy soils as compared to other members of *Macroteropsis* since most collecting sites were located within large dune formations, such as the Samalayuca sand dunes south of El Paso, Texas, and a dune system running northward from Deming to Hatch, New Mexico (Brown & Lowe 1980).

Phenology – August and September.

Floral associations – The male holotype was collected on *Kallstroemia*, but all of the other 94 specimens were collected on *Sphaeralcea* sp., in particular, *S. incana*. *P. magniceps* is clearly a *Sphaeralcea* oligolege since pollen-laden females carry *Sphaeralcea* pollen in their scopae. *S. incana* is a distinctive species of *Sphaeralcea* that grows up to two meters in height. Like *P. magniceps, S. incana* is restricted to very dry, sandy localities in New Mexico and northern Mexico (Martin & Hutchins 1981), suggesting that these two species form a close association.

Perdita (*Macroteropsis*) *portalis* Timberlake

(Plates I and II; Figs. 36b, 42, 43, 45)

Perdita (*Macroteropsis*) *portalis* Timberlake, 1954:357 [description and key]; 1956:323 [additional material]; 1960:125 [additional material]; 1962:27 [key]; 1968:4 [new record]; 1980:5 [description of macrocephalic male]; 1980:3 [key].

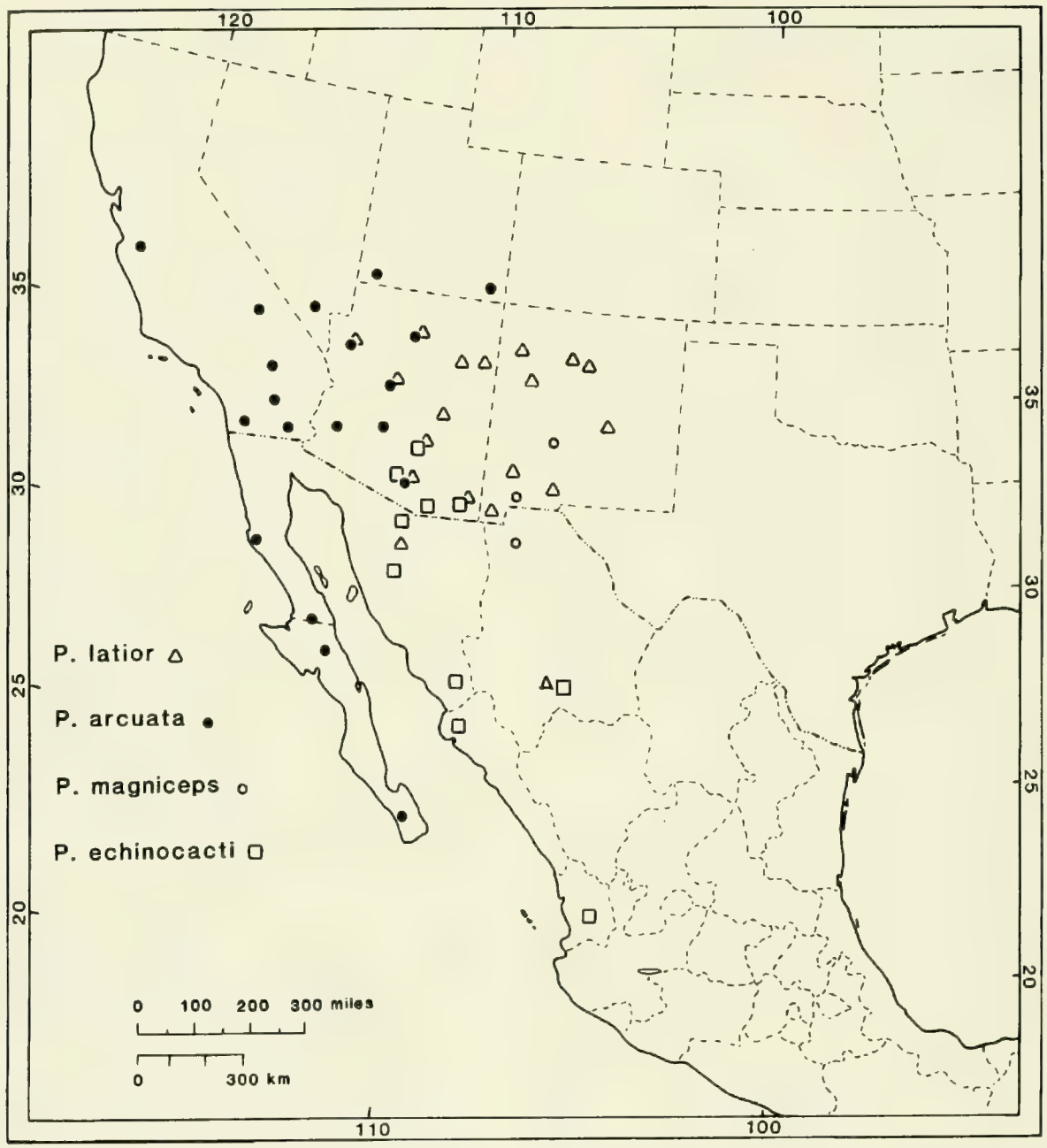


Fig. 41. Geographic distributions of species in the subgenus *Macroteropsis*, in part.

Type material – The male holotype and allotype are located in the CAS (Type No. 14670). The types were collected at Portal, Cochise Co., Arizona, August 12, 1940, on *Sphaeralcea,* (Timberlake, coll.).

Diagnosis – Forewing length 2.7 - 3.4 mm. This species and *P. haplura* are the smallest in *Macroteropsis.* Males of these two species are similar in having greatly enlarged, apparently glandular, facial foveae (black in *P. haplura* and cream colored in *P. portalis*), strongly protuberant, grey-blue eyes which are convergent below, elongate, thick, white erect setae over the vertex, meso- and metanotum (as well as the usual fine, recumbent pilosity), an acutely pointed clypeus which hangs over the base of the labrum (in the smallest specimens this feature can be weakly developed) and a broad, spade-like S8 (Fig. 42e). Furthermore, males have a conspicuous, acute inner tooth at the apex of the mandibles. Males of these two species can be distinguished based on the color of the facial foveae (see above), size (*P. portalis* smaller than *P. haplura*), the shape of T7 (apex more slender in *P. portalis* [Fig. 42g] than in *P. haplura* [Fig. 44e]) and the genital capsule (cuspis expanded in *P. haplura* and with extensive papillae over upper surface). Female *P. portalis,* like *P. haplura,* have a black head and mesosoma covered with scattered, erect, finely-branched, white setae and a fuscous metasoma. *P. portalis* can be distinguished from *P. haplura* by the presence of yellow maculation on the fore-

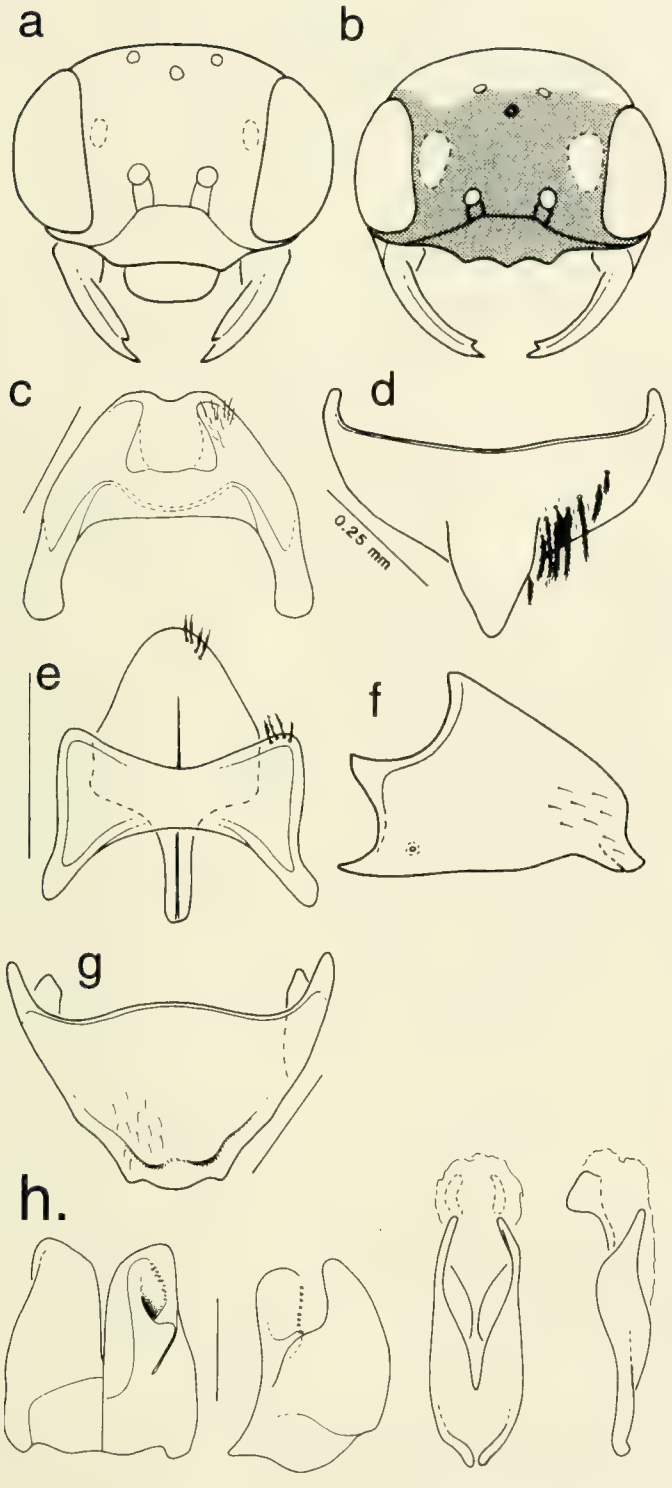


Fig. 42. *Perdita portalis.* **(a)** female head, **(b)** male head, **(c)** female S6, **(d)** female T6, **(e)** male S7 and S8, **(f)** male T7, lateral view, **(g)** male T7, dorsal view, **(h)** male genital capsule (dorsal, ventral and lateral views), aedeagus (dorsal and lateral view).

tibia, by the weaker convergence of the eyes ventrally, by the shape of S6 and by the more slender, acutely pointed pygidial plate.

A pair of male specimens, collected at Gray mountain, Coconino Co., Arizona, July 26, 1952 by M. Cazier and R. Schrammel, differ from the majority of the *P. portalis* specimens in the structure of the genital capsule and T7. The apex of the genital capsule is more quadrate and the mesal margins of the volsellae are obtusely produced (Fig. 43a). The apex of the male T7, which possesses a broad, blunt protuberance in typical *P. portalis,* bears an acute, horizontal shelf (Fig. 43b). One of these males was seen by Timberlake (1956:323). In the absence of more material from this locality I see no reason to consider these specimens a different species from *P. portalis;* more likely they simply represent the extreme of the morphological variation in this species.

P. portalis, like *P. mellea,* has dimorphic males. The male referred to in the diagnosis is the typical flight-capable male most common in collections (Plate I). However, in 1970, J.G. Rozen, Jr., discovered in nests a flightless, macrocephalic male morph (described by Timberlake, 1980:5-6) (Plate II). The behavior and morphology of this bizarre and highly derived male morph is described elsewhere (Danforth, 1991b).

Distribution – Semidesert/grassland regions of Cochise, Graham, Coconino counties, Arizona; Luna, Hidalgo, Socorro, Otero, Chaves, Eddy, Quay counties, New Mexico; Hudspeth Co., Texas; Zacatecas and Coahuila states, Mexico (Fig. 45). Additional specimens are recorded from Chihuahua and Durango, Mexico by PCAM (Ayala, et al., 1996), but I have not examined these specimens myself.

Phenology – July through September.

Floral associations – The majority of specimens were collected on *Sphaeralcea* (*angustifolia, laxa*), (79 females/29 males) and this is clearly the predominant pollen source for this species, but some specimens have been collected on *Aplopappus* (2 males) and *Tidestromia lanuginosa* (1 female).

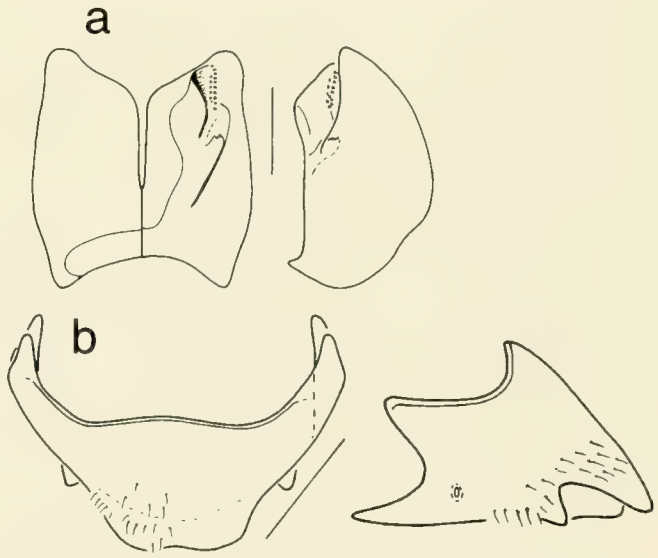


Fig. 43. *Perdita portalis* (variant form). **(a)** male genital capsule (dorsal, ventral and lateral views), **(b)** male T7, dorsal and lateral views.

Perdita (*Macroteropsis*) *haplura* Cockerell

(Figs. 44, 45)

Perdita haplura Cockerell, 1922a:19 [description of female].

Perdita (*Macroteropsis*) *haplura:* Timberlake, 1954:357; 1960:124 [redescription of female]; 1962:87 [description of male]; 1968:4 [additional material]; 1980:3 [key].

Type material – The holotype female is in the NMNH (Type No. 24896). The type was collected at Sanderson, Terrell Co., Texas, May 9, 1912 (J.D. Mitchell, coll.).

Diagnosis – Forewing length 3.2 - 4.0 mm. Males of *P. haplura* and *P. portalis* share greatly enlarged, apparently glandular, facial foveae (black in *P. haplura* and cream colored in *P. portalis*), strongly protuberant, grey-blue eyes (in pinned specimens) which are convergent below, elongate, thick, white, erect setae over the vertex, meso- and metanotum (as well as the usual fine, recumbent pilosity), an acutely-pointed clypeus which hangs over the base of the labrum (in the smallest specimens this feature can be weakly developed), a broad, spade-like S8 (Fig. 44d) and elongate, bifid mandibles. These two species can be distinguished based on the features given above (in the diagnosis of *P. portalis*). Female *P. haplura*, like *P. portalis*, have a black head and mesosoma with scattered, erect, finely branched setae and a fuscous metasoma. The density of the white mesosomal setae will distinguish these two species from all other members of *Macroteropsis*. *P. haplura* can be distinguished from *P. portalis* by the lack of yellow maculation on the foretibiae, by the stronger convergence of the eyes ventrally (Fig. 44a), by the shape of S6, and by the broader, less acutely pointed pygidial plate.

Distribution – Desert/grassland habitats of Lincoln and Dona Ana counties, New Mexico; Terrell, Pecos, Val Verde counties, Texas (Fig. 45).

Phenology – April through May and September.

Floral associations – Collected primarily on *Sphaeralcea* (*angustifolia* var. *cuspidata*) (5 females/4 males), but also on *Fallugia paradoxa* (1 female).

Subgenus *Cockerellula* Strand

Lutziella Cockerell, 1922c:1.

Cockerellula Strand 1932:196; Timberlake 1953:963-968 [key to species, additional species]; 1954:354 [description, key to species]; 1956:323 [additional species]; 1960:122-123 [key to males; additional species]; 1968:2-4 [key to males, additional species]; 1980:1-2 [additional species].

Type species – *Perdita opuntiae* Cockerell, by original designation for *Lutziella* and autobasic for *Cockerellula*.

Diagnosis – This subgenus can be distinguished from the other subgenera treated here by the following combination of characters: (1) un-segmented, latero-apical projection on side of gonocoxite, (2) extremely slender S7, (3) modifications of male S1-S3 (in some species), (4) female metasoma reddish, (5) 6-segmented maxillary palpus, (6) second labial palpal segment arising apically on first, and (7) apodemes of the penis valves curving dorsad.

Perdita (*Cockerellula*) *azteca* Timberlake

(Figs. 36c, 46, 50)

Perdita (*Cockerellula*) *azteca* Timberlake, 1954:355 [description]; 1954:354 [key]; 1960:122 [key]; 1968:2 [key].

Type material – Holotype male and allotype are in the CAS (Type No. 14438). They were collected at Zimapan, Hidalgo, Mexico, June 11, 1951 (P.D. Hurd, coll.).

Diagnosis – Forewing length 3.6 - 4.0 mm. With *P. opuntiae* this is the largest species of *Cockerellula*, with forewing lengths reaching 4.0 mm. Males are easily distinguished from all other close relatives by the uniquely-shaped seventh tergum, with paired blunt prongs extending dorso-posteriorly from the posterior margin (Fig. 46d), by the hind tibial spurs, which have particularly long teeth on the inner surface, which gives them a pectinate appearance, and by the male genital capsule (Fig. 46f). In addition, males have a unique combination of sternal modifications: the first sternum is produced medially into a pucker-like fold, and S2 and S3 have obtuse transverse protuberances along their posterior margins (strongest on S3) (Fig. 62a). Females can be recognized by the presence of a raised triangular area between the antennal

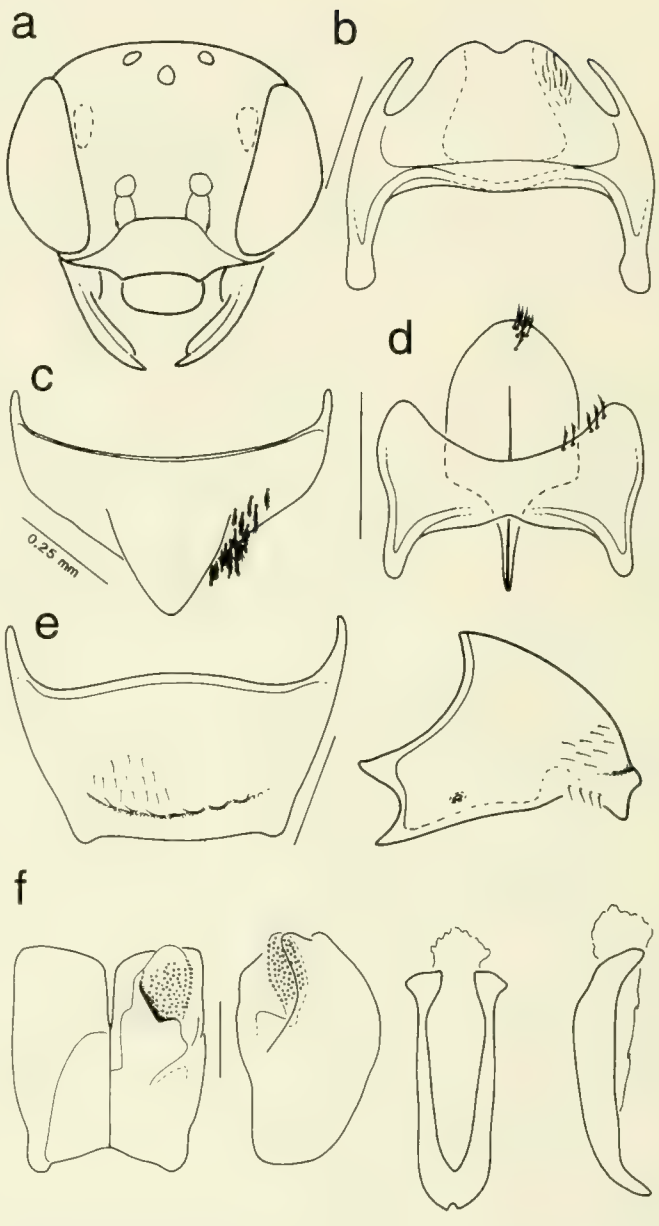


Fig. 44. *Perdita haplura.* **(a)** female head, **(b)** female S6, **(c)** female T6, **(d)** male S7 and S8, **(e)** male T7, dorsal and lateral views, **(d)** male genital capsule (dorsal, ventral and lateral views), aedeagus (dorsal and lateral view).

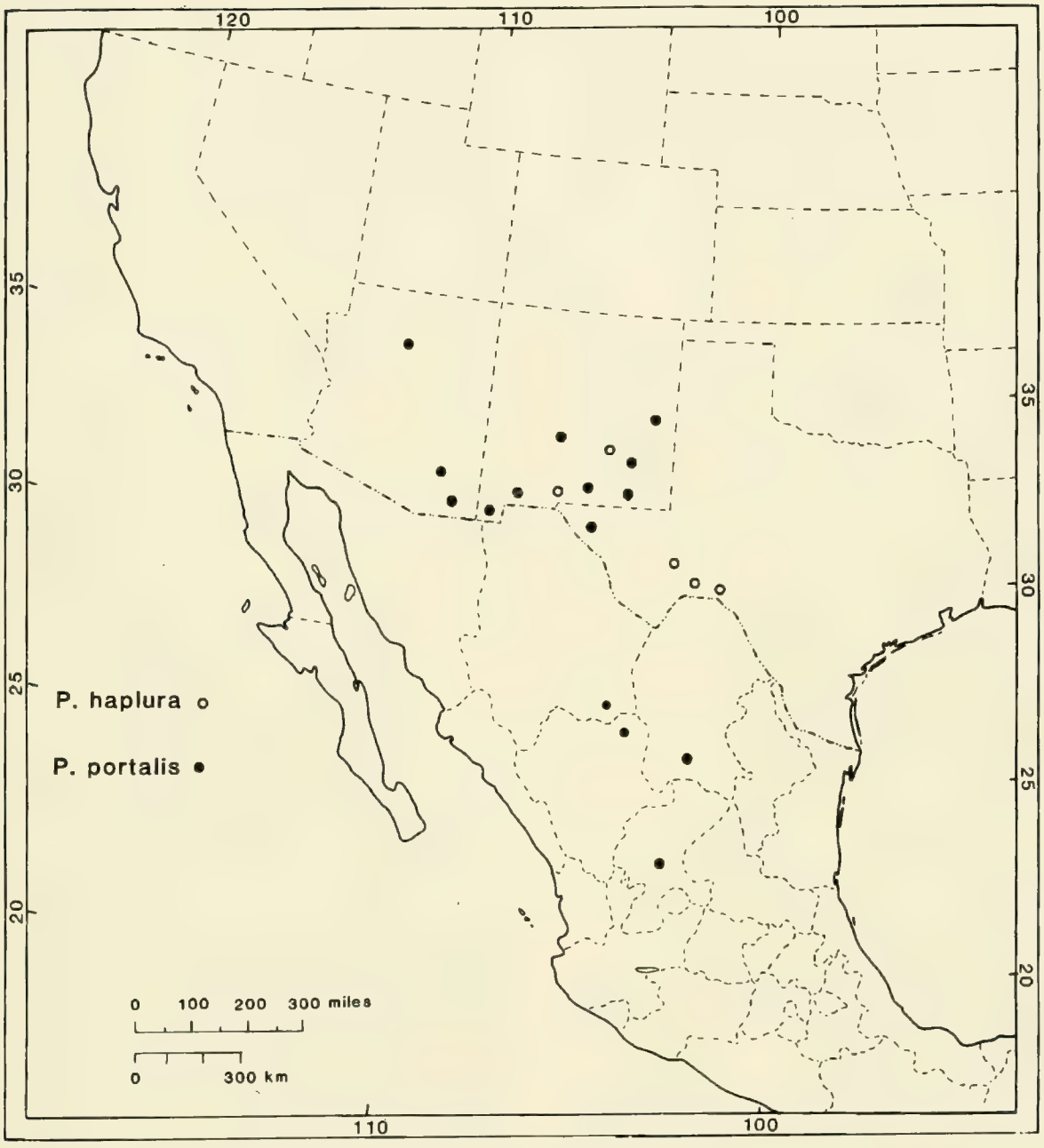


Fig. 45. Geographic distributions of species in the subgenus *Macroteropsis*, in part.

sockets which extends down to the lateral corners of the clypeus. On the postero-lateral surfaces of the propodeum there are patches of dense, finely-branched, white setae, which are present in only a few other species, and the female mandibles are particularly bright yellow. The pygidial plate is especially broad and blunt in *P. azteca* (e.g., in comparison to *P. knulli* and *P. bidenticauda* (Fig. 46b), and S6 is uniquely shaped also (Fig. 46a).

Distribution – States of Hidalgo, San Louis Potosí, Jalisco, Puebla and Oaxaca, Mexico; up to 8100 ft. in elevation (Fig. 50).

Phenology – March through July, and rarely into September.

Floral associations – Collected exclusively on Cactaceae: *Opuntia* (25 females/16 males), *Eysenhardtia polystachya* (7 females), *Echinocactus* (2 females) and *Ferrocactus* (1 male).

Perdita (*Cockerellula*) *bidenticauda* Timberlake

(Figs. 47, 50)

Perdita (*Cockerellula*) *bidenticauda* Timberlake, 1953:965 [description]; 1953:964 [key]; 1954:356; 1954:354 [key]; 1960:122 [key]; 1968:2 [key].

Type material – The male holotype is at KU. The holotype was collected at Cooper's Store, Big Bend National Park, Brewster Co., Texas, April 11, 1947, on *Opuntia* (Michener and Beamer, coll.).

Diagnosis – Forewing length 2.8 - 3.2 mm. Males of this species can be recognized by the T7 shape, which has paired, postero-apical processes, as in *P. azteca,* however much less well developed. The presence of obtuse transverse protuberances along the posterior margin of S2 and S3 (more pronounced on S3) and the *lack* of a pucker like fold on S1 will further distinguish this species. In the key to *Cockerellula,* Timberlake states that *P. bidenticauda* and *P. laticauda* are indistinguishable in the female sex (1954:355). I have found no characters which allow one to distinguish them. These two species may be distinguished from all others by the shape of the female S6, with the elongate central fused area and the deeply divided lateral portions (Fig. 47a).

Distribution – This species is known only from the type locality (Fig. 50).

Phenology – April.

Floral associations – All paratype and the holotype specimens (2 females/6 males) were collected on *Opuntia* flowers.

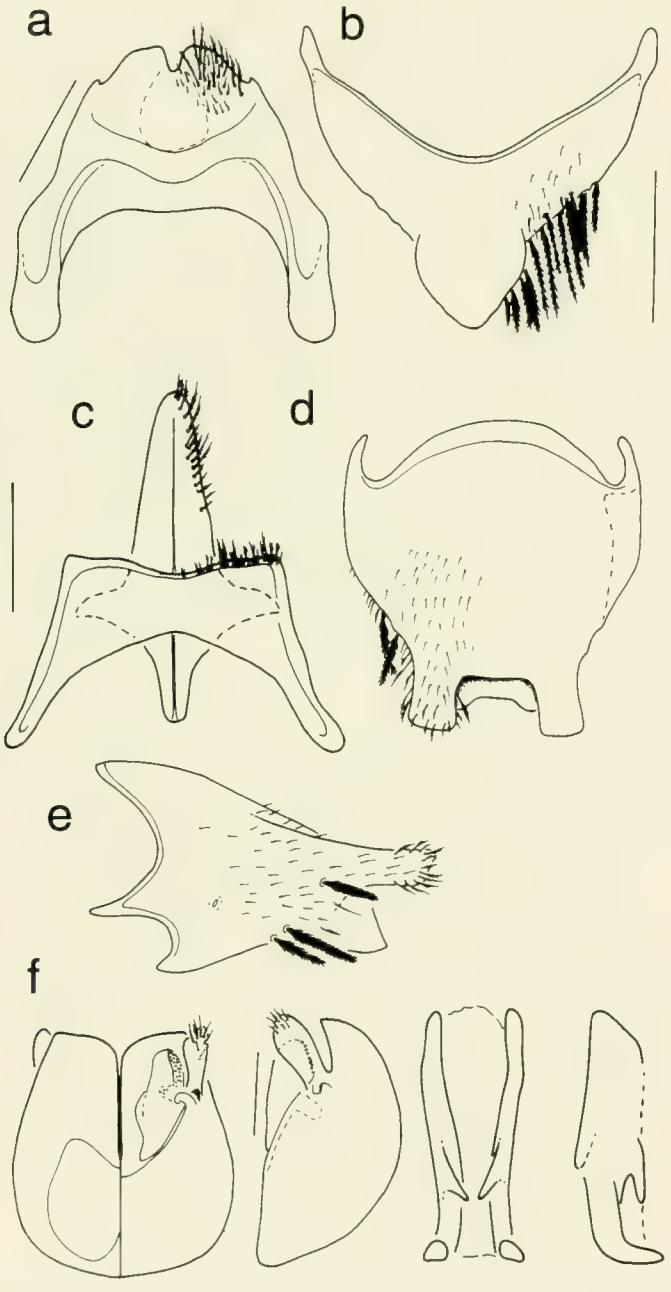


Fig. 46. *Perdita azteca.* **(a)** female S6, **(b)** female T6, **(c)** male S7 and S8, **(d)** male T7, dorsal view, **(e)** male T7, lateral view, **(f)** male genital capsule (dorsal, ventral and lateral views), aedeagus (dorsal and lateral view).

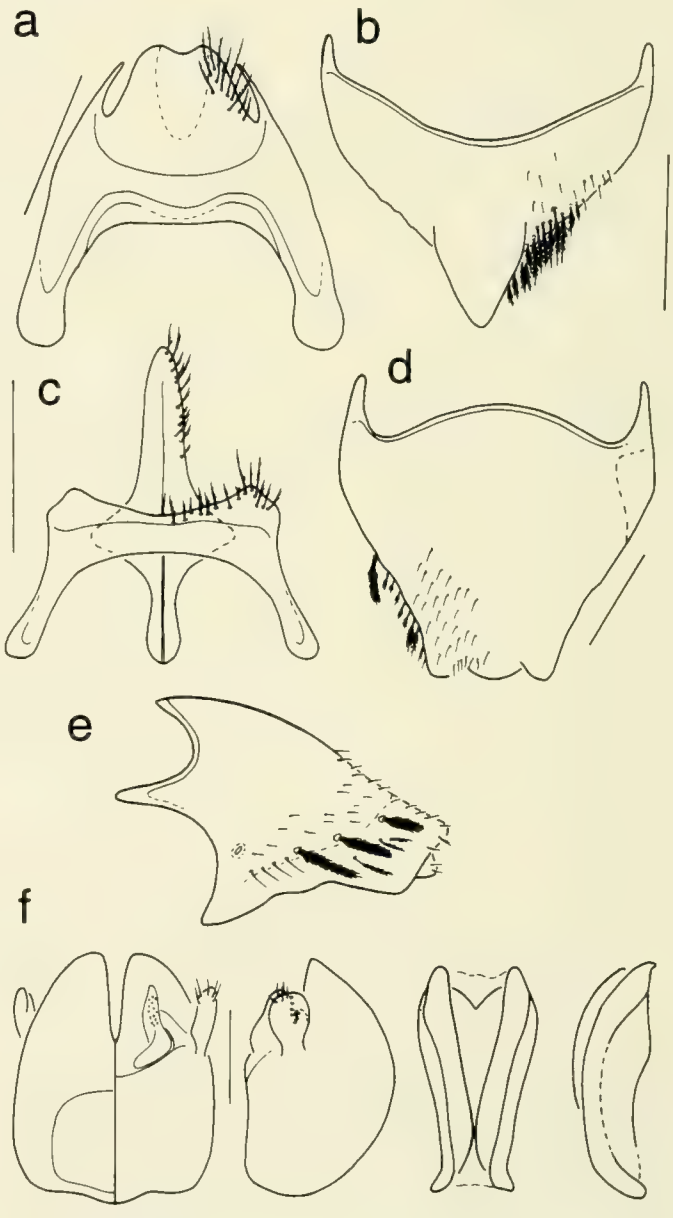


Fig. 47. *Perdita bidenticauda.* **(a)** female S6, **(b)** female T6, **(c)** male S7 and S8, **(d)** male T7, dorsal view, **(e)** male T7, lateral view, **(f)** male genital capsule (dorsal, ventral and lateral views), aedeagus (dorsal and lateral view).

Perdita (*Cockerellula*) *knulli* Timberlake

(Figs. 48, 50)

Perdita (*Cockerellula*) *knulli* Timberlake, 1960:123 [description]; 1960:122 [key]; 1968:2 [key].

Type material – The male holotype and allotype are located at OhS. Both were collected in the Davis Mts., Jeff Davis Co., Texas, June 21, 1949 (D.J. and J.N. Knull, colls.).
The female allotype bears similar labels.

Diagnosis – Forewing length 2.6 - 3.0 mm. Males can be distinguished by the narrowly bidentate apex of T7. S1 is produced medially into a pucker-like lobe (which will distinguish this species from *P. bidenticauda*) and S2 has paired diverging ridges which end at the posterior margin of the sternum in minute prongs or points. These are similar to the structures on the second sternum in *P. opuntiae,* but are less strongly protuberant. Female *P. knulli* can be recognized by the unique combination of very small size (wing length < 3.0 mm), reddish metasoma, and thick, dense erect setae on lateral surface of propodeum. The head and thorax are entirely dark, and have a distinct greenish sheen.

Distribution – Jeff Davis, Brewster and Pecos, Texas; Luna Co., New Mexico. Additional specimens from Mexico were collected by Terry Griswold and others at two localities (Ojinaga and Mapimi) in the states of Chihuahua and Durango; up to 4700' (Fig. 50).

Phenology – April to June and August to November (in the southern-most locality).

Floral associations – *Opuntia* (1 female/1 male) and *Acacia* (2 males); in Mexico, *Argemone turneri* (7 females/10 males) and *Opuntia imbricata* (3 females/2 males).

Perdita (*Cockerellula*) *rubida* Timberlake

(Figs. 49, 50)

Perdita (*Cockerellula*) *rubida* Timberlake, 1968:2 [description of male]; 1968:2 [key].

Type material – The male holotype is reported to have been deposited in the CAS, but there is no record of this species in their type catalog or in the collection, nor is this specimen in the UCR collection. The holotype male was collected at 9 miles south of San Juan del Rio, Durango, Mexico, Aug. 21, 1960 (Arnaud, Ross, Rentz, colls.).

Diagnosis – Forewing length is 2.6-2.8 mm. This is the smallest *Cockerellula* species. Males can be easily recognized based on the paired, dorso-ventrally directed prongs arising preapically on the seventh terga. These are similar to prongs seen in *P. azteca* but more slender and acutely pointed. Metasomal sterna lack modifications seen in other members of this group. Yellow maculation on the face of males reaches the antennal sockets medially, but unlike all other close relatives, maculation extends above the antennal sockets along the inner margins of the eyes laterally. The background coloration of the head and metasoma is black with a metallic blue sheen. Females are entirely black with a metallic blue tinge to the head and mesosoma. The female S6 is similar to that of *P. azteca.* Timberlake did not have any female specimens of this species when he described it.

Although I have not seen the male holotype, nor any other specimens identified by Timberlake, I have two specimens, a male and a female, found in the undetermined *Perdita* collection of the AMNH, which appear to belong to this species. The male specimen agrees in all respects to Timberlake's description, except the AMNH specimen lacks any small fold along the posterior margin of S1, a feature Timberlake noted for the holotype. The shape of the S1 could easily vary depending on the condition of the specimen, and so I do not consider this discrepancy reason for describing the AMNH specimens as a new species.

Description – FEMALE – Head: (1) width 1.32 mm; (2) 1.1 times broader than long (as measured from the vertex to the lower margin of the clypeus); (3) clypeus weakly imbricate, shiny, with distinct punctation; (4) frons imbricate to granulate with distinct, widely scattered punctures and with linear depression along midline; (5) vertex imbricate-punctate; (6) gena imbricate with scattered punctures; (7) head except clypeus and central, raised triangular area between antennae distinctly bluish-green; (8) whole head clothed in fine, white, minutely branched setae, especially dense on genae, vertex and paraoccular areas; (9) inner margins of eyes subparallel, diverging slightly below; eyes brownish; (10) posterior ocelli slightly above upper margin of com-

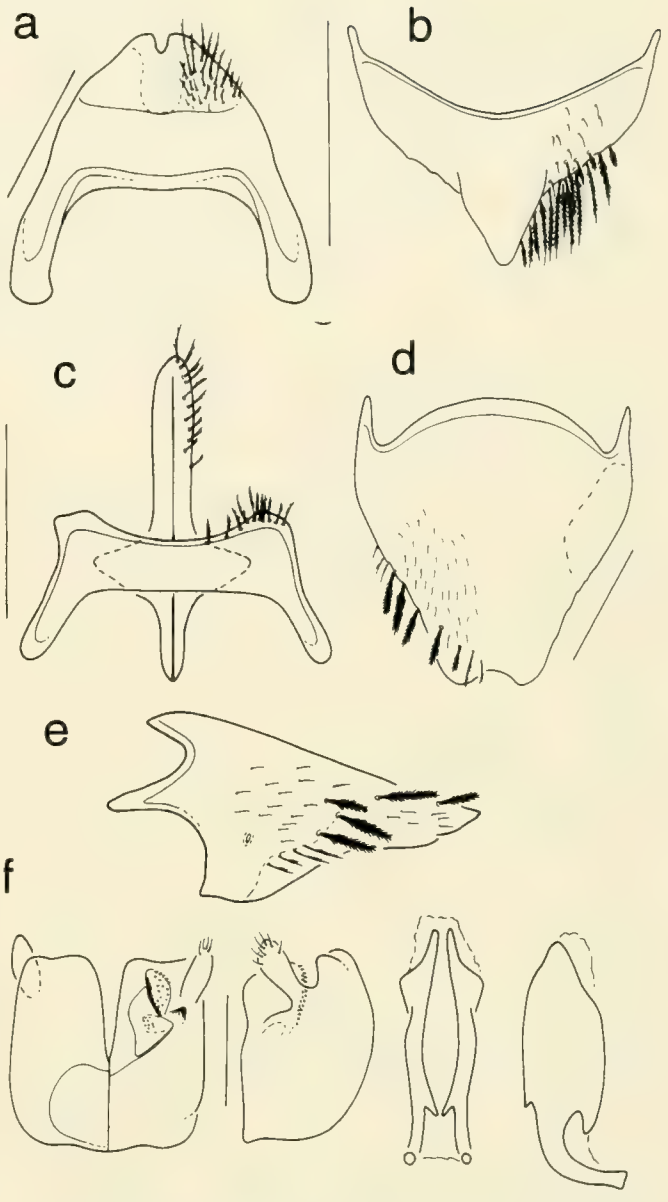


Fig. 48. *Perdita knulli.* **(a)** female S6, **(b)** female T6, **(c)** male S7 and S8, **(d)** male T7, dorsal view, **(e)** male T7, lateral view, **(f)** male genital capsule (dorsal, ventral and lateral views), aedeagus (dorsal and lateral view).

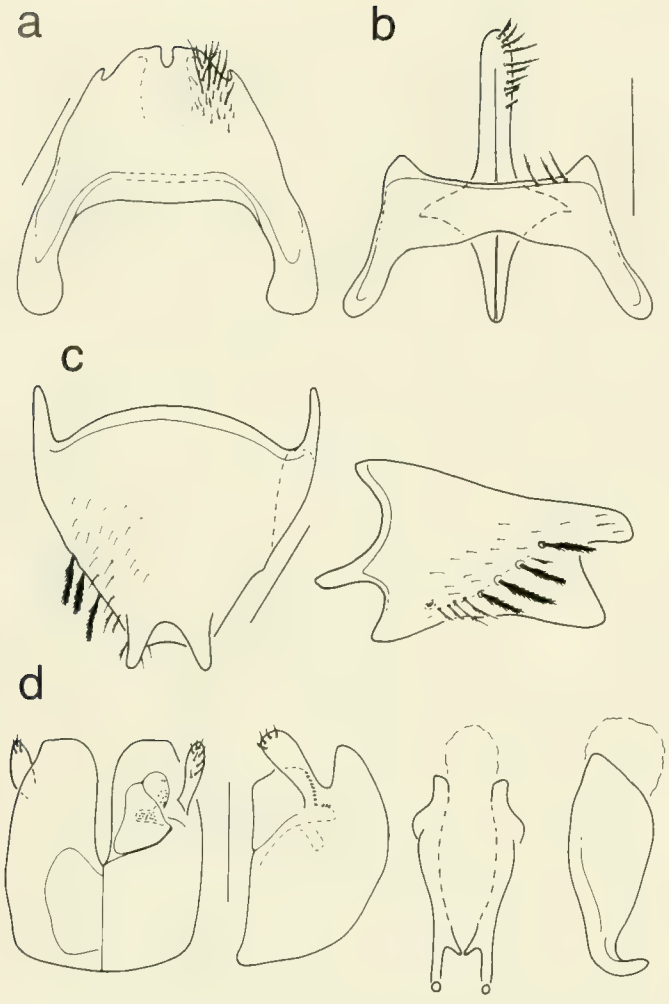


Fig. 49. *Perdita rubida.* **(a)** female S6, **(b)** male S7 and S8, **(c)** male T7, dorsal and lateral views, **(d)** male genital capsule (dorsal, ventral and lateral views), aedeagus (dorsal and lateral view).

pound eye; lateral ocelli one ocellar width from central ocellus; (11) facial foveae distinct; 0.6 mm in length and slightly expanded above; (12) scape of antenna equal in length to flagellar segments 1-5, first and second flagellar segments equal in length.

Mouthparts: (13) labrum with central depressed area flanked by erect, finely branched setae and distal transverse ridge; apical margin with long, simple setae (14) mandible brown, becoming rufous apically; with distinct pre-apical tooth and sulcus originating at mandibular acetabulum and extending diagonally across base of mandible; (15) glossa elongate, roughly 1.2 times longer than prementum; (16) paraglossa slender basally but expanding distally into broad, brushlike apex; (17) labial palpus 4-segmented, first segment twice length of remaining segments combined and second segment inserted apically on first; (18) galeal comb short, consisting of only 6-7 small setae at proximal end of galea; (19) maxillary palpus 6-segmented, all segments distinct and well developed; palpus almost equal in length to distal part of galea.

Mesosoma: (20) pronotum brownish with faint bluish tinge dorsally; coriarious-imbricate dorsally, with weak punctures, becoming more distinctly coriarious laterally; (21) mesoscutum with distinct metallic blue-green sheen; surface finely imbricate and appearing dull, with weak punctures and mixture of erect, white, finely branched setae and smaller, silver, recumbent setae; notauli weakly developed, parapsidal lines and central longitudinal sulcus present; (22) mesoscutellum and metanotum similar in coloration, sculpturing and setae; (23) mesopleuron distinctly bluish; sculpturing finely alveolate dorsally, gradually changing to imbricate laterally; scrobal sulcus absent; (24) metapleuron imbricate; (25) propodeum distinctly and deeply alveolate dorsally, with weak rugae at propodeal-metanotal suture, becoming imbricate laterally; with small patches of erect, white setae separating the dorsal and lateral surfaces, as in other *Cockerellula;* entire propodeum bluish; (26) intertegular distance 0.92 mm; (27) forewing length 2.80 mm; wings translucent; veins brown; (28) legs brown, no yellow maculation evident; (29) basitibial plate distinct, quadrate apically, with a few stout recumbent setae on its concave surface; (30) scopal hairs on anterior surface of tibia simple, becoming finely branched along outer edge of tibia; (31) midtibial spur finely serrate and gradually curving to apex; (32) inner hind tibial spur distinctly longer than outer; both finely serrate; (33) tarsal claws all bifid.

Metasoma: (34) terga dark brown (35) terga 1-5 minutely imbricate with small posteriorly-directed, recumbent setae and a very few long, erect, finely branched setae laterally; (36) deeply impressed fovea on lateral edge of T2; (37) T5 with long, erect, plumose setae arising on distal 1/2 of tergum and small, median patch of finely branched setae on distal margin of tergum; (38) graduli on terga 2-4; lateral portions of graduli visible on T2 and T3; (39) T6 with raised, acutely pointed pygidial plate flanked by dense, plumose setae; central portion of pygidial plate colliculate; (40) sterna light brown; S1-5 similar in sculpturing and vestiture to terga except with a few long, finely branched setae ventrally; (41) S6 with apical slender notch and small lateral emarginations giving rise to two apico-lateral prongs (Fig. 49a); (42) sternal graduli lacking on all segments except S1, where they are present only laterally.

Distribution – Grant Co., New Mexico (AMNH specimens) and Durango, Mexico (holotype male) (Fig. 50). Additional specimens are recorded from Sonora, Mexico by PCAM (Ayala, et al., 1996), but I have not examined these specimens myself.

Phenology – August; up to 2100 m. elevation.

Floral associations – unknown.

Perdita (*Cockerellula*) *laticauda* Timberlake

(Figs. 51, 53)

Perdita (*Cockerellula*) *laticauda* Timberlake, 1953:967 [description]; 1953:964 [key]; 1954:356 [additional material]; 1960:122 [key].

Type material – The male holotype and allotype are at KU, and were collected 15 miles southeast of Dryden, Terrell Co., Texas, April, 13 1949, on *Gilia acerosa* (Michener and Beamer, colls.).

Diagnosis – Wing length 3.0 - 3.2 mm. This species is the sister species to *P. lobata.* Males of both of these species can be recognized based on the unique combination of a protuberant S1 (produced into a pucker like fold) and a rectangular patch of setae along the posterior margin of S3 (Fig. 62c). In both species the posterior margin of T7 is dorso-ventrally compressed, with sharp apico-lateral corners, and concave ventrally. This species can be distinguished from *P. lobata* based on the coloration of the head and mesosoma and posterior margin of the male T7. Male *P. lobata* have paler, more reddish head and mesosoma coloration, while in *P. laticauda* the background coloration of the head and mesosoma is dark brown with bluish metallic sheen. Furthermore, in *P. lobata* the posterior margin of T7 is more strongly emarginate

Fig. 50. Geographic distributions of species in the subgenus *Cockerellula*, in part.

medially and the lateral corners are bent further ventrally. The genital capsule of these two species is very similar, but in *P. lobata* the apical margin of the gonocoxites are produced medially, in ventral view, while in *P. laticauda* the apical margin is more or less straight. Finally, in *P. lobata* the papillae extend almost all the way to the apex of the cuspis, while in *P. laticauda* the papillae are further removed from the apex of the cuspis, restricted to the basal 1/2, in dorsal view. Female *P. laticauda*, *P. lobata* and *P. bidenticauda* are very difficult to distinguish, and one must rely on associations with males collected at the same locality.

Distribution – Terrell and Webb counties, Texas; Coahuila, Mexico (Fig. 53).

Phenology – April in Texas and August in Mexico.

Floral associations – *Gilia acerosa* (9 females/11 males), *Chamaesaracha conioides* (6 females/2 males), *Opuntia* (1 male) and *Gaillardia* (1 female).

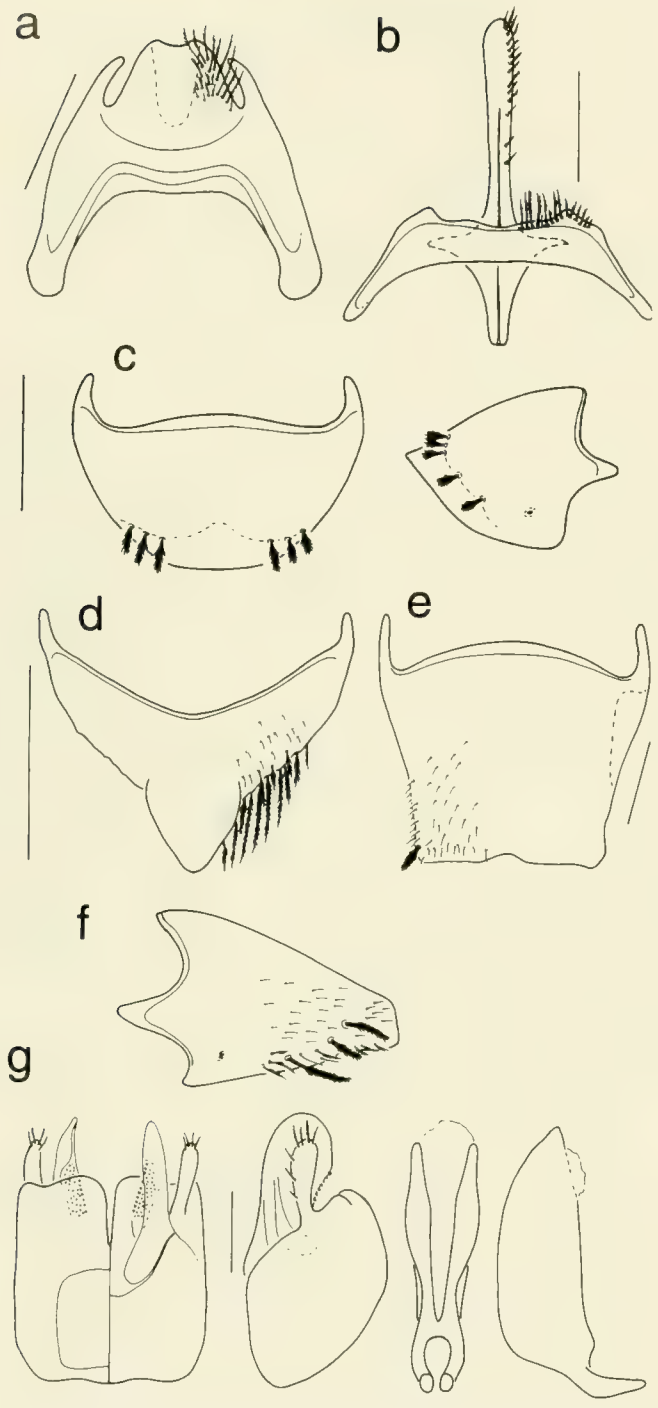


Fig. 51. *Perdita laticauda.* **(a)** female S6, **(b)** male S7 and S8, **(c)** male T6, dorsal and lateral views showing erect, moss-like setae, **(d)** female T6, dorsal view, **(e)** male T7 dorsal view, **(f)** male T7, lateral view, **(g)** male genital capsule (dorsal, ventral and lateral views), aedeagus (dorsal and lateral view).

***Perdita* (*Cockerellula*) *lobata* Timberlake**

(Figs. 52, 53)

Perdita (*Cockerellula*) *lobata* Timberlake, 1953:967 [description, male]; 1953:964 [key]; 1954:356; 1954:354 [key]; 1960:122 [additional material, including female specimens, but no description of female].

Type material – The male holotype is located at KU, and was collected 15 miles northwest of Mission, Hidalgo Co., Texas, March 30, 1946, on *Opuntia* (C.D. Michener, coll.).

Diagnosis – Forewing length 3.0-3.2 mm. This species is very similar to *P. laticauda.* See above for features which allow them to be distinguished.

Distribution – Starr and Hidalgo counties, Texas (Fig. 53).

Phenology – March.

Floral associations – *Opuntia* (2 males).

***Perdita* (*Cockerellula*) *opuntiae* Cockerell**

(Figs. 54, 58)

Perdita (*Lutziella*) *opuntiae* Cockerell, 1922c:2 [description]; Custer, 1928:67-84; 1929a:50-51; 1929b:294-295 [biology].

Perdita (*Cockerellula*) *opuntiae:* Timberlake, 1953:964 [key]; 1954:355

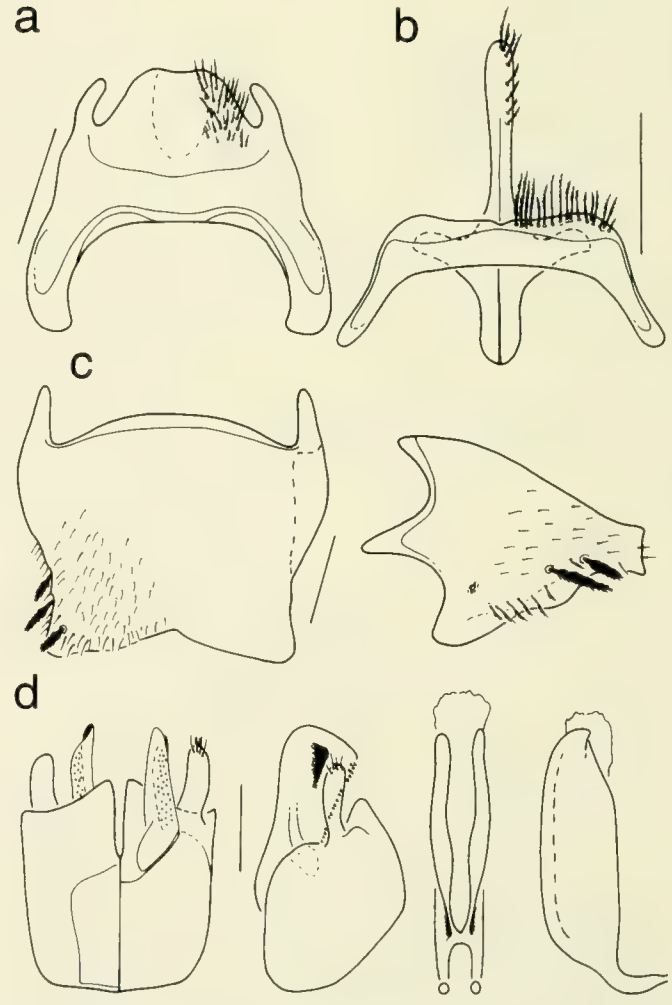


Fig. 52. *Perdita lobata.* **(a)** female S6, **(b)** male S7 and S8, **(c)** male T7, dorsal and lateral views, **(d)** male genital capsule (dorsal, ventral and lateral views), aedeagus (dorsal and lateral view).

[additional material]; 1954:354 [key]; 1960:122 [key]; Bennett & Breed, 1985:185-194 [biology].

Type material – The male holotype is located in the CAS (Type No. 15443). The holotype was collected at White Rocks, Boulder, Boulder Co., Colorado, June 13, on *Opuntia* (W.P. Cockerell, coll.).

Diagnosis – This species, along with *P. azteca* and *P. seminigra*, are the largest species of *Cockerellula* (forewing length = 3.6 - 4.0 mm). Males are easily recognized by the shape of T7, with two latero-apical prongs separated by a wide emargination, and the presence of a broad, quadrate protuberance on the posterior margin of the S2. The female head and mesosoma are much lighter in coloration than in the similarly-sized *P. azteca*, and possess dense patches of yellowish-white setae on the postero-lateral surface of the propodeum. Scopal hairs are longer and denser than in *P.*

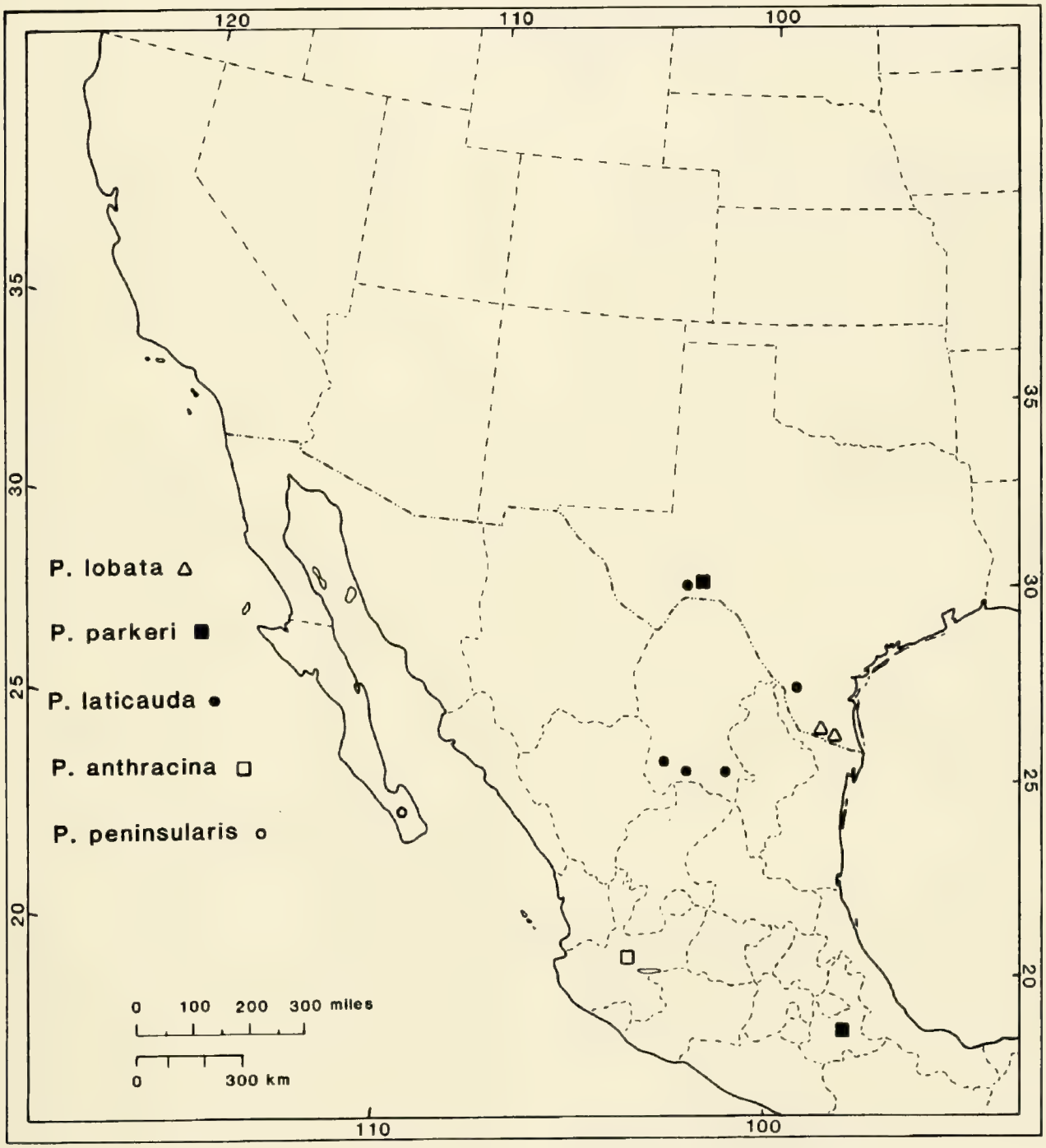


Fig. 53. Geographic distributions of species in the subgenus *Cockerellula*, in part.

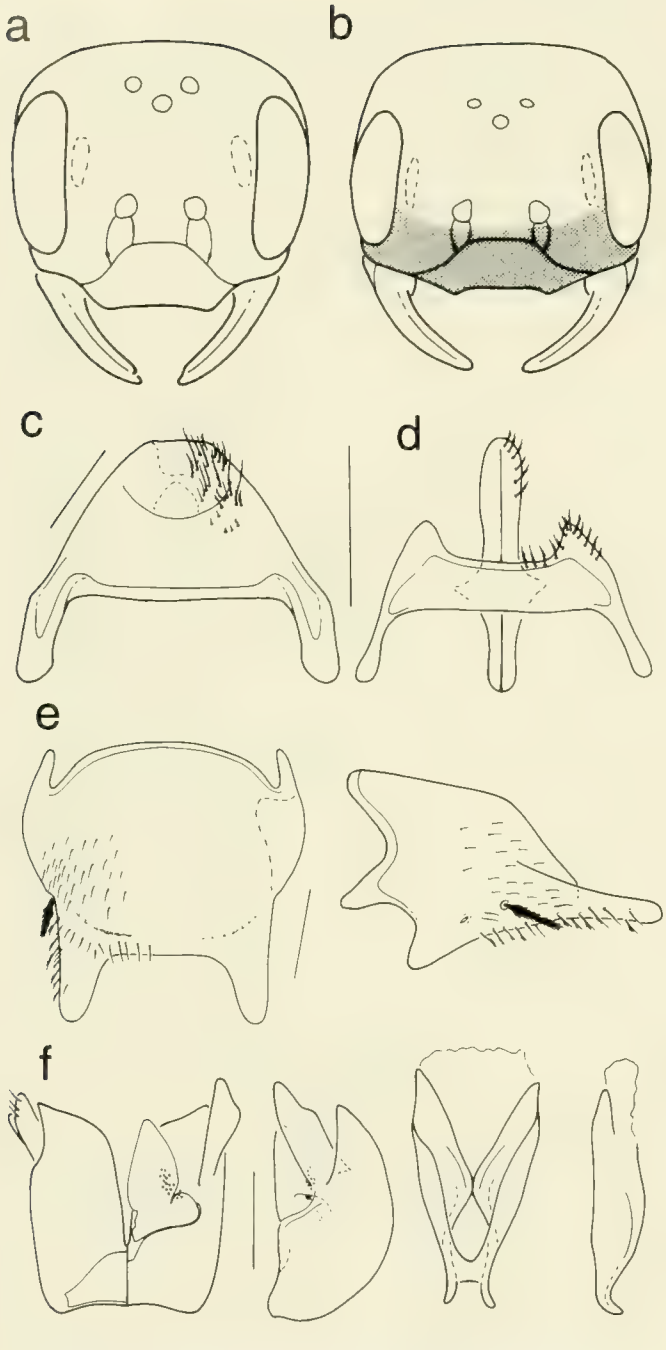


Fig. 54. *Perdita opuntiae.* **(a)** female head, **(b)** male head, **(c)** female S6, **(d)** male S7 and S8, **(e)** male T7, dorsal and lateral views, **(f)** male genital capsule (dorsal, ventral and lateral views), aedeagus (dorsal and lateral view).

azteca. The shape of the female S6 should serve for positive identification: the transparent area is divided in two in *P. opuntiae* (Fig. 54c).

Distribution – Known primarily from White Rocks, a Laramie sandstone formation located 11 km northeast of Boulder, Colorado, although one male was collected in Shannon Co., South Dakota [Timberlake, 1954:355] (Fig. 58).

Phenology – June through July.

Floral associations – Pollen collection is restricted to *Opuntia compressa* and *O. polycantha* (Bennett and Breed, 1985).

Perdita (*Cockerellula*) *parkeri* Timberlake

(Figs. 53, 55)

Perdita (*Macroteropsis*) *parkeri* Timberlake, 1980:4 [description of female]; 1980:3 [key].

Type material – The female holotype is located in the CAS (Type No. 14656), and was collected at Cacaloapan, Puebla, Mexico, April 26, 1962 (F.D. Parker, coll.).

Diagnosis – This species is known only from the holotype and two additional specimens collected by Jack Neff in Blanco Co., Texas. The male is very similar to *P. opuntiae* except that the mesonotum and mesopleura are more dull (they are shining in *P. opuntiae*), and the head and thorax are black (they are light brown in *P. opuntiae*). The female of this species shows a number of characteristics that indicate it is more closely related to members of *Cockerellula* than to species of *Macroteropsis:* the head is only 1.1 times wider than long (rather than 1.3 times in *Macroteropsis*), the lateral surfaces of the propodeum have dense patches of setae, as in female *P. azteca* and *P. opuntiae,* the maxillary palpi are six-segmented and the segments are all much longer than wide, and the second labial palpal segment inserts apically on the first. Females of this species differ from all others in *Cockerellula* in the the striate (or lineolate; Timberlake, 1980) sculpturing of the dorsal surface of the propodeum, in the shape of S6 (Fig. 55a), and in the dark coloration of T1.

This species was heretofore known only from the female. The description of the male given below is based on a single male collected along with a female by Jack Neff.

Description – MALE – Head: (43) width 1.84 mm; (44) 1.35 times broader than long; (45) clypeus broad, imbricate and weakly punctate; (46) frons coarsely granulate, unusually dull, with shallow punctures; (47) vertex similar but more distinctly punctate; (48) gena imbricate-punctate; (49) head black with creamy white maculation on clypeus, subantennal plates and paraoccular area extending upward along inner margin of eye to between eye and facial fovea; sharp border between yellow and black areas; very weak reddish metallic sheen on frons; (50) head nearly bare; few, short setae on frons and vertex; (51) inner margins of eyes strongly divergent below; (52) posterior ocelli separated from occipital margin by 0.4 mm; (53) facial fovea distinctly impressed, slender, 0.30 mm in length; (54) antennae light brown; scape equal in lenth to first six flagellar segments.

Mouthparts: (55) labrum yellow, 2.4 times broader than long; shallow, concave depression along proximal margin; (56) mandible yellow with reddish tip; apex simple, no sub-apical tooth; (57) glossa normal, equal to prementum in length; (58) paraglossae slender and acutely pointed; (59) labial palpus normal, 4-segmented, with the first segment longer than remaining segments combined; (60) galeal comb absent; (61) maxillary palpus 6-segmented, second segment elongate, as in other members of the *Macrotera* group.

Mesosoma: (62) pronotum brown, imbricate; thick white setae across dorsum, extending to pronotal lobes; (63) mesoscutum densely granulate with large, shallow punctures as on head; parapsidal lines distinct, unusually deeply impressed, 0.32 mm in length; notauli absent; (64) sculpturing of mesoscutellum and metanotum similar to mesoscutum; metanotum with erect white setae laterally and along posterior margin; (65) mesopleuron with distinctly imbricate, scale-like sculpturing; scrobe deeply impressed; scroal sulcus lacking; erect, widely-scattered setae over surface; (66) metapleuron similar but without setae; (67) lateral surface of propodeum alveolate; lateral and dorsal or posterior surface sep-

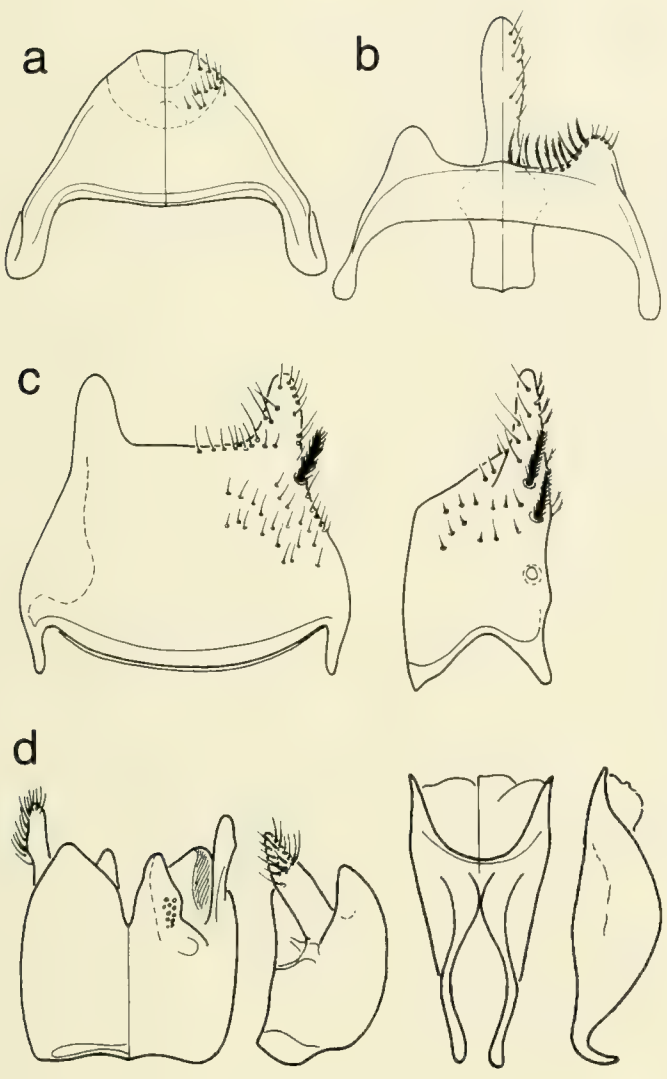


Fig. 55. *Perdita parkeri.* **(a)** female S6, **(b)** male S7 and S8, **(c)** male T7, dorsal and lateral views, **(d)** male genital capsule (dorsal, ventral and lateral views), aedeagus (dorsal and lateral view).

arated by row of setae that are erect and widely separated dorsally, becoming shorter and much more closely-spaced ventrally (toward junction of metanotum) to form a discrete patch of setae; dorsal surface of propodeum of propodeal triangle deeply alveolate; lateral alveoli roughly quadrate while those along midline are laterally compressed giving the propodeum a slightly lineolate or striate appearance, as in female; (68) intertegular distance 1.16 mm; (69) forewing length 3.64 mm; wing veins light brown; stigma dark brown; venation pattern roughly as in female except veins Cu1a and 2m-cu slightly weaker than others; (70) legs dark brown except for apex of forefemur and anterior surface of foretibia, which are light brown/yellowish; (71) basitibial plate distinct; surface imbricate with 6-8 punctures; no setae covering surface; (72) outer surface of hind tibia with erect, moss-like setae intermixed with slender, white setae; (73-74) mid- and hindtibial spurs finely serrate and hooked at apex; (75) tarsal claws all bifid.

Metasoma: (76) terga all bright red; (77) T1-T7 smooth with minute punctation and inconspicuous, recumbent white setae; (78) single row of stout setae across T6; (79) longitudinal fovea on lateral surface of T2; (80) T7 divided apically into paired prongs separated by 0.45 mm (similar to *P. opuntiae*); (81) graduli present on T2-T6; graduli on T2 and T3 especially well-developed with lateral portions visible; (82-83) sterna similar in coloration, punctation and vestiture to terga; (84) S2 with paired acute projections from posterior surface extending out of plane of sternum; (85) S7 elongate and slender, S8 narrow (as in Fig. 55b); (86) genital capsule quadrate in dorsal view, with ventro-lateral projections (Fig. 55d) as in other *Cockerellula;* (87) volsellar cuspis compressed laterally; (88) papillae along dorsal surface of cuspis; (89) penis valves diverging apically, as in *P. seminigra* and *P. opuntiae* (Fig. 55d).

Distribution – Blanco Co., Texas south to Puebla, Mexico (Fig. 53). The specimens collected by Jack Neff greatly expand the known range of this species.

Phenology – April.

Floral associations – The holotype bears no flower record but the specimens collected in Texas were on *Opuntia.*

Perdita (*Cockerellula*) *seminigra* Timberlake

(Figs. 56, 58)

Perdita (*Cockerellula*) *seminigra* Timberlake, 1956:323 [description of male]; 1960:122 [key].

Type material – The male holotype is in the CAS (Type No. 14705), and was collected 34 miles south Acatlan, Puebla, Mexico, 6000', July 10, 1952 (E.E. Gilbert and C.D. MacNeill, colls.).

Diagnosis – This species is known only from the holotype specimen. Forewing length 3.6 mm. The male of this species is very similar to that of *P. opuntiae.* Both species are large (forewing length > 3.6 mm) and have brownish heads and mesosomas, and fuscous metasomas. The facial maculation in *P. seminigra,* however, is whiter than in *P. opuntiae* and is restricted to the paraocular areas, between the outer subantennal sulcus and the compound eye up to the level of the antennal sockets. In both

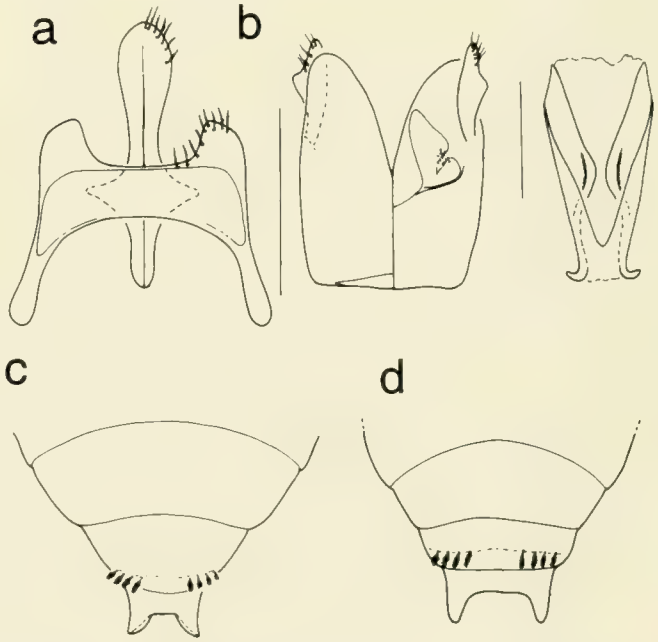


Fig. 56. *Perdita seminigra.* **(a)** male S7 and S8, **(b)** male genital capsule (dorsal and ventral views), aedeagus (dorsal view), **(c)** apex of male metasoma in *P. seminigra* as compared to **(d)** *P. opuntiae.*

species, the male S2 has a broad, quadrate protuberance (broader in *P. opuntiae* [width = 0.5 mm] than in *P. seminigra* [width = 0.32 mm]) and the male T7 has two, large, latero-apical prongs along the posterior margin which are separated by a wide, concave emargination. The prongs are more widely separated in *P. opuntiae* (distance between apices of two prongs roughly 0.56 mm) than in *P. seminigra* (0.48 mm), and in *P. seminigra* there is a distinct flange on the inner margin of each prong (Fig. 56c). The setae over the metanotum and lateral surface of the propodeum are shorter and less dense in *P. seminigra*. The penis valves and genital capsules of *P. opuntiae* and *P. seminigra* are also very similar.

Distribution – Known only from the type locality (Fig. 58).

Phenology – July.

Floral associations – unknown.

Perdita (*Cockerellula*) *solitaria* Cockerell

(Figs. 36d, 57, 58)

Perdita solitaria Cockerell, 1897b:152 [description of female]; Cockerell, 1922b:1 [new locality].

Perdita (*Macroteropsis*) *solitaria:* Timberlake, 1954:365; 1954:361 [key]; 1968:7 [key].

Perdita (*Cockerellula*) *quadridentata* Timberlake 1980:1 [description of male] NEW SYNONYMY.

Perdita (*Macroteropsis*) *atrella* Timberlake 1968:4 [description of female]; 1980:3 [key] NEW SYNONYMY.

Type material – The female holotype is located in the NMNH (Type No. 3384). The holotype was collected at Soledad Canon, Organ Mountains, Dona Ana Co., New Mexico, August 15 (C.H.T. Townesend, coll.). The male holotype and allotype of *P. quadridentata* are in the CAS (Type No. 14680), and were collected 5 miles east of Nogales, Santa Cruz Co., Arizona, September 1, 1970, on *Baccharis* (G.E and R.M. Bohart, colls.). The female holotype of *P. atrella* is in the CAS (Type No. 14434) and was collected 20 miles south Estacion Llano, Sonora, Mexico, August 18, 1964 (M.E. Irwin, coll.).

Diagnosis – Forewing length 2.4 - 2.6 mm. Males are most easily recognized by the uniquely-shaped T7, with two converging dorso-apically directed prongs and two diverging latero-apical prongs (Fig. 57). Both males and females can be distinguished from other close relatives by the unusually proportioned labial palpi: segments 2-4 are long and thin and their total combined length is equal to the first segment (Fig. 36d). Females are entirely dark, lacking reddish metasomal coloration, the body is sparsely clothed in elongate, erect setae and there is no metallic sheen to the head or mesosoma.

P. atrella and *P. quadridentata* appear to be junior synonyms of *P. solitaria*. *P. quadridentata* was based on the male of *P. solitaria*, as judged by a male specimen collected along with females of *P. solitaria* at Sycamore Canyon, Santa Catalina Mts., Pima Co., Arizona, 20 August, 1916. Timberlake (1954:365) was unaware of this male specimen when he treated *P. solitaria* as a species known only from the female. Cockerell (1922b:1) does not mention this male specimen, although he did report having seen two females from the same locality and date. The female allotype of *P. quadridentata* is indistinguishable from females of *P. solitaria*.

P. atrella is also a junior synonym of *P. solitaria;* the type agrees in all respects with *P. solitaria*. Because Timberlake (1968:4) compared the holotype specimen of *P. atrella* to species of *Macroteropsis* rather than *Macroterella* (which contained *P. solitaria*), he was lead to the incorrect conclusion that it was a new species.

Distribution – Pima, Cochise and Santa Cruz counties, Arizona; Dona Ana Co., New Mexico and Sonora, Mexico (Fig. 58); collected up to 3800 ft. (in Santa Catalina Mts.)

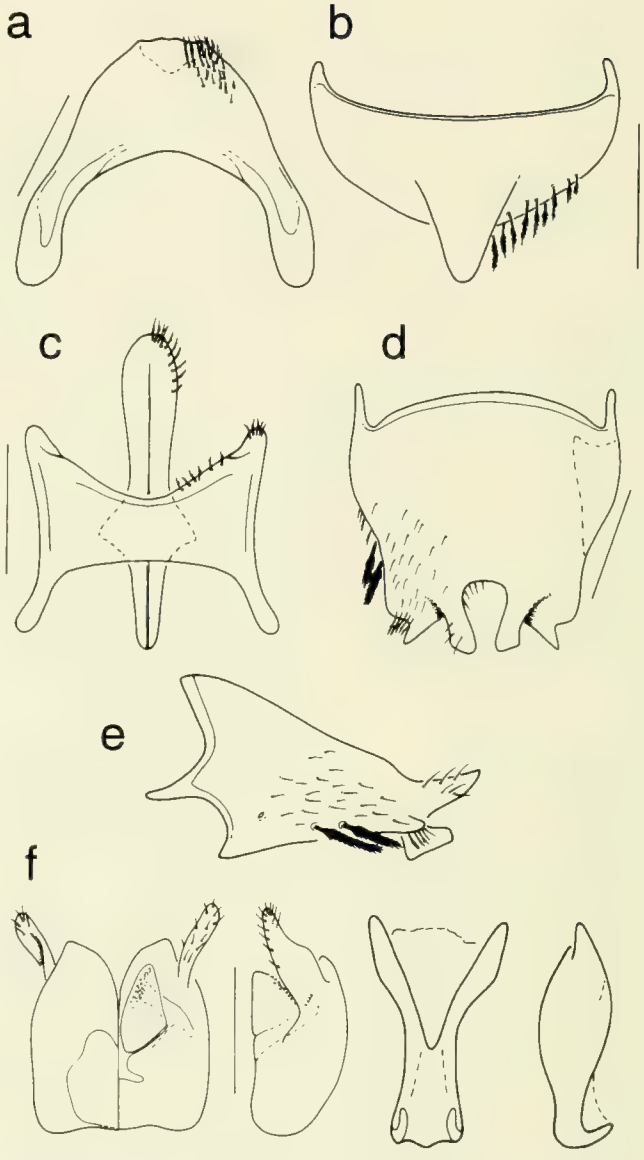


Fig. 57. *Perdita solitaria.* **(a)** female S6, **(b)** female T6, **(c)** male S7 and S8, **(d)** male T7, dorsal view, **(e)** male T7, lateral view, **(f)** male genital capsule (dorsal, ventral and lateral views), aedeagus (dorsal and lateral view).

Phenology – August to September.

Floral associations – Collected on *Baccharis* (holotype male and allotype) and on *Eriogonum abertianum neomexicanum* (1 female).

Perdita (*Cockerellula*) *anthracina* Timberlake

(Figs. 53, 59)

Perdita (*Macroteropsis*) *anthracina* Timberlake, 1980:3 [description of female and key].

Type material – The female holotype is in the CAS (Type No. 14422), and was collected 10 miles north of Guadalajara, Jalisco, Mexico, October 16, 1968 (G.E. Bohart, coll.).

Diagnosis – This species is known only from the holotype fe-

Fig. 58. Geographic distributions of species in the subgenus *Cockerellula*, in part.

male. Forewing length 3.4 mm. The body is entirely black with a faint coppery sheen on the head and mesosoma; and scattered, long, erect setae. Wing veins are brown. The female is superficially similar to female *Macroteropsis*, but lacks the mouthpart characters of that group. The holotype female lacks dense patches of setae on the lateral surface of the propodeum.

Distribution – Jalisco, Mexico (Fig. 53).

Phenology – May.

Floral Associations – unknown.

***Perdita* (*Cockerellula*) *peninsularis* Timberlake**

(Figs. 53, 59)

Perdita (*Cockerellula*) *peninsularis* Timberlake, 1968:3 [description of female].

Perdita (*Macroteropsis*) *peninsularis:* 1980:2; 1980:3 [key].

Type material – The holotype female is located in the CAS (Type No. 12993), and was collected at Triunfo, Baja California Sur, Mexico, July 7, 1938 (Michelbacher and Ross, coll.).

Diagnosis – Forewing length 3.4 mm. This species is known from only two female specimens collected at the type locality on 7 and 13 July, 1938. Timberlake originally placed it in the subgenus *Cockerellula* but in 1980 (p.2), he transferred it to the subgenus

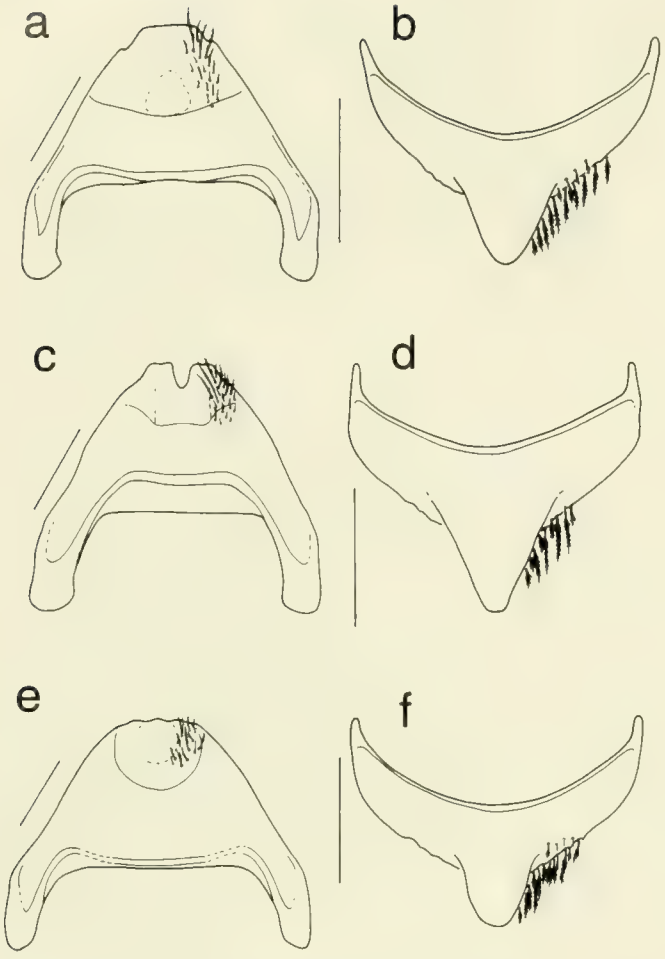


Fig. 59. *Perdita anthracina.* **(a)** female S6, **(b)** female T6. *Perdita penninsularis.* **(c)** female S6, **(d)** female T6. *Perdita robertsi.* **(e)** female S6, **(f)** female T6

Macroteropsis, without giving any explanation for this change. I have since seen all of Timberlake's material from the CAS, and in this material were one male and one female, collected 6 mi. NW El Rosario, near Consuelo, Baja California, Mexico on 18 May, 1965 by D.Q. Cavagnaro, C.E. and E.S. Ross and V.L. Vesterby, which were identified by Timberlake as *P. peninsularis.* Based on dissections of these specimens it is clear that they are really *P. arcuata.* In fact, in the CAS *P. arcuata* material is another female specimen with the same locality data which he had identified as *P. arcuata.* I believe that by mistaking these specimens of *P. arcuata* as *P. peninsularis* he made the incorrect decision to transfer *P. peninsularis* to *Macroteropsis.*

Based on the two female *P. peninsularis*, this species clearly belongs in *Cockerellula.* Females have relatively long faces (width only 1.1 times length), elongate, well-developed maxillary palpi, and the second labial palpus arises apically on the first. The body is entirely black, with fine imbricate-punctate sculpturing over much of the head and metasoma and scattered, erect white setae. Wing veins are brown. The propodeal triangle is finely areolate and the lateral surfaces of the propodeum bear erect, plumose, white setae, similar to the setae on the propodea of *P. opuntiae* or *P. azteca*, but less dense. This species can be most easily distinguished from the other *Cockerellula* by the conspicuously concave basitibial plate, the shape of the female S6 (deeply divided apically), and pygidial plate (elongate and slender with narrowly quadrate apex; Fig. 59d).

Distribution – Baja California Sur, Mexico (Fig. 53).

Phenology – July.

Floral associations – unknown.

Perdita (Cockerellula) robertsi Timberlake

(Figs. 50, 59)

Perdita (Macroteropsis) robertsi Timberlake, 1968:6 [description of female]; 1980:3 [key].

Type material – The female holotype is in the CAS (Type No.

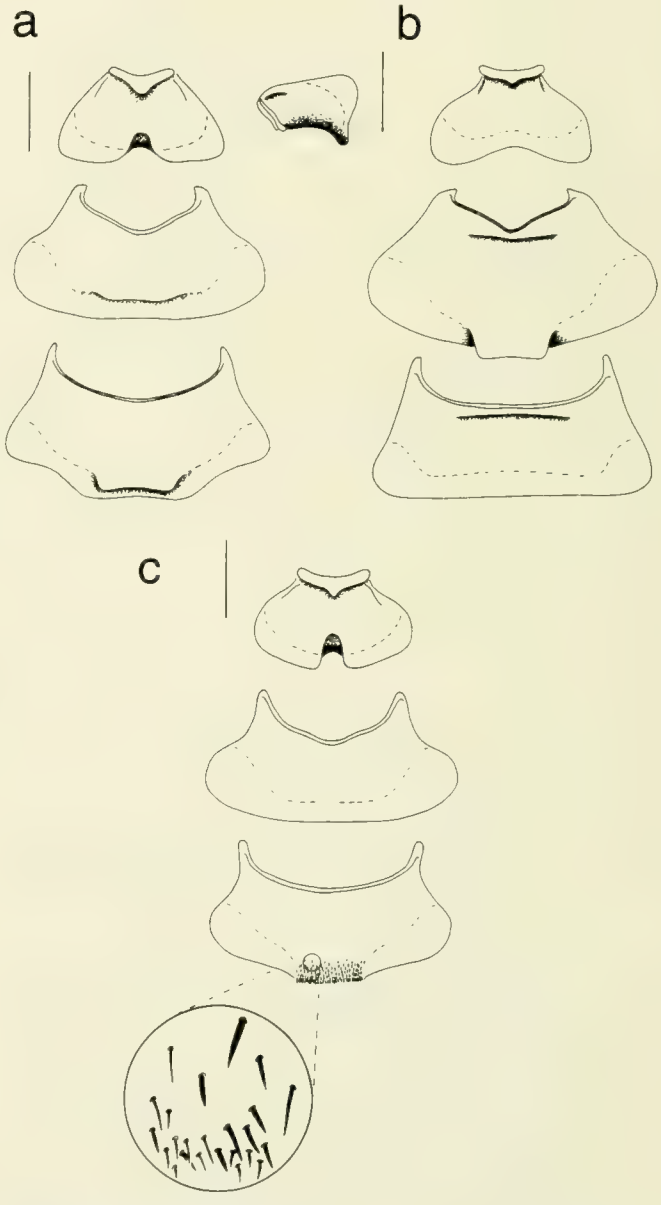


Fig. 60. Male sterna 1 through 3. **(a)** *Perdita texana*, **(b)** *Perdita echinocacti.*

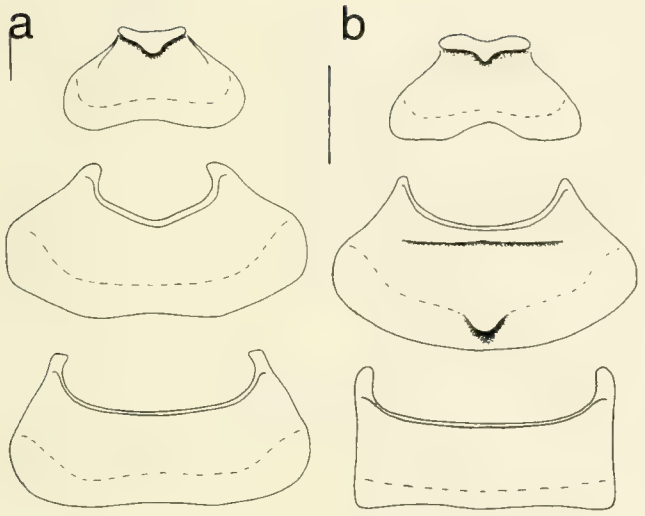


Fig. 61. Male sterna 1 through 3. **(a)** *Perdita azteca,* **(b)** *Perdita opuntiae,* **(c)** *Perdita lobata.*

14687). This specimen was collected at Pecos River Canyon, 38 miles north west Del Rio, Val Verde Co., Texas, 13 April 1963 (R.B. Roberts, coll.).

Diagnosis – Forewing length 3.7 mm. This species is known from the holotype and four additional female specimens collected by John Neff. Although originally placed in *Macroteropsis,* this specimen lacks the characters of that group and possesses a number of features of the subgenus *Cockerellula:* the head is scarcely longer than wide, the maxillary palpi are well developed and six-segmented, the second labial palpal segment arises apically on the first, the metasoma is reddish and there are two dense patches of thick, white setae on the lateral surfaces of the propodeum, as in *P. azteca.* The yellow maculation on the paraocular areas, immediately above the mandibular bases, and S6 shape will distinguish females of this species from all others in the subgenus.

Distribution – Val Verde Co., Texas (Fig. 50).

Phenology – April.

Floral associations – Although the holotype lacks a flower record, Timberlake (1968) suggested that it was most likely collected on *Opuntia.* John Neff's specimens were collected in Val Verde Co., Texas (as was the holotype) on *Opuntia engelmannii* and *Echinocereus enneacanthus.*

Heteroperdita Timberlake

Perdita (*Heteroperdita*) *pilonotata* Timberlake

Perdita (*Macroterella*) *pilonotata* Timberlake, 1980:6 [description].

Type material – I was unable to locate the holotype female.

Diagnosis – Forewing length 2.0 mm. This species clearly belongs in the subgenus *Heteroperdita* and is thus not part of the *Macrotera* complex. The characters which unite *P. pilonotata* with other species in *Heteroperdita* include: (1) hypostomal region of female, on either side of proboscidial fossa, with elongate, posteriorly directed setae, (2) although lacking yellow maculation present in other members of this group, female with short, appressed white setae on the frons, the scuto-scutellar suture and the metanotum, (3) portion of male S8 beyond apodemes (disc of the male S8) quadrate and blunt apically and male genital capsule resembling other species of *Heteroperdita.*

Distribution – NEW MEXICO: Otero Co., 3900 ft., 21 Aug., 1962; Catron Co., 16 mi. S. Datil, 16 June, 1956; Valencia Co., Correo, 15 June, 1956 (Timberlake, 1980:7).

ACKNOWLEDGMENTS

I am grateful to Dr. Charles D. Michener for his excellent support and guidance at all points throughout this work. I thank the members of my Ph.D. committee, David Alexander, William J. Bell, George W. Byers, Rudolf Jander and Edward O. Wiley, for their critical comments on the manuscript and for their help throughout my graduate tenure at the University of Kansas.

I am very grateful to the Smithsonian Institution for a Pre-Doctoral Fellowship at the National Museum of Natural History. Ronald J. McGinley provided excellent advice and oversight, and generously shared his office and resources with me during my stay.

I thank the following people and institutions for providing specimens for this study and for allowing me to work in their collections: Jerome G. Rozen, Jr., and Eric Quinter, American Museum of Natural History (AMNH); Wojciech Pulawski, California Academy of Sciences (CAS); Roy R. Snelling, Los Angeles County Museum of Natural History (LACM); Ronald McGinley, National Museum of Natural History, Smithsonian Institution (NMNH); Ohio State University, Columbus (OhS); James DiGiulio, Oregon State University (OrS); Howell V. Daly, University California, Berkeley (UCB); Lynn Kimsey, R.M. Bohart Museum of Entomology, University of California, Davis (UCD); Saul I. Frommer, University of California, Riverside (UCR); U.N. Lanham, University of Colorado Museum, Boulder (UColB); Charles D. Michener and Robert W. Brooks, Snow Entomological Museum, University of Kansas, Lawrence (KU); and Ricardo Ayala and Gregorio Rodriguez, Estacion de Biologia Chamela, Universidad National Autonoma de Mexico (UNAM) (Acronyms used follow McGinley, 1986). Additional specimens for this study were provided as a result of collecting trips organized by the Programa Cooperativo sobre la Apifauna Mexicana (PCAM) and funded by the National Science Foundation (Wallace E. LaBerge & Ronald J. McGinley, Principal Investigators, NSF BFR 90-24723). I am grateful to Doug Yanega for providing locality data for PCAM specimens.

Natalya Florenskya generously provided the half-tone illustrations (Plates I and II).

LITERATURE CITED

Ashmead, W.H. 1899. Classification of the bees, or the superfamily Apoidea. Trans. Am. Entomol. Soc. 26:49-100.

Ayala, R., T.L. Griswold, & D. Yanega. 1996. Apoidea (Hymenoptera). In: Llorente, J.E., A.N. García-Aldrete, & S.E. González (Eds.), Biodiversidad, taxonomía y biografía de artrópodos de Mexico: Hacia una síntesis de su conocimiento (pp. 423-464), Mexico: Instituto de Biología, Universidad National Autonoma de México.

Bennett, B. & M.D. Breed. 1985. The nesting biology, mating behavior and foraging ecology of *Perdita opuntiae* (Hymenoptera: Andrenidae). J. Kansas Entomol. Soc. 58:185-194.

Brooks, R.W. 1988. Systematics and phylogeny of the anthophorine bees (Hymenoptera: Anthophoridae; Anthophorini). Univ. Kansas Sci. Bull. 53:436-575.

Brown, D.E. & C.H. Lowe. 1980. Biotic communities of the southwest. USDA Forest Service Technical Report RM-78, 1p. (map). Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

Cockerell, T.D.A. 1896. The bees of the genus *Perdita* F. Smith. Proc. Acad. Nat. Sci. Phila. 48:25-107.

Cockerell, T.D.A. 1897a. New and little-known north American bees. Proc. Acad. Nat. Sci. Phila. 49:334-355.

Cockerell, T.D.A. 1897b. New and little-known bees. Trans. Am. Entomol. Soc. 24:144-162.

Cockerell, T.D.A. 1904. New and little-known bees in the collection of the British Museum. Ann. Mag. Nat. Hist. (Ser. 7)14:203-208.

Cockerell, T.D.A. 1905. Notes on some bees in the British Museum. Trans. Am. Entomol. Soc. 31:309-364.

Cockerell, T.D.A. 1922a. Bees in the collection of the United States National Museum - 4. Proc. U.S. Nat. Mus. 60:(Art. 18)1-20.

Cockerell, T.D.A. 1922b. Bees of the genus *Perdita* from the western states. Amer. Mus. Novitates 33:1-15.

Cockerell, T.D.A. 1922c. Two new subgenera of North American bees. Am. Mus. Novitat. 47:1-5.

Cockerell, T.D.A. & W. Porter. 1899. Contributions from the New Mexico Biological Station. VII. Observations on bees, with descriptions of new genera and species. Ann. Mag. Nat. Hist. (Ser.7)4:403-421.

Cresson, E.T. 1878. Descriptions of new North American Hymenoptera in the collection of the American Entomological Society. Trans. Am. Entomol. Soc. 7:61-136.

Custer, C.P. 1928. The bee that works stone: *Perdita opuntiae* Cockerell. Psyche 35:67-84.

Custer, C.P. 1929a. Habits of *Perdia zebrata* with description of larva. Canadian Entomol. 61:49-51.

Custer, C.P. 1929b. Notes on the cocoons and parasites of *Melissodes obliqua* and nests of *Perdita opuntiae* (Hymenoptera-Apoidea). Psyche 36:293-295.

Danforth, B.N. 1989a. The evolution of hymenopteran wings: the importance of size. J. Zool., London 218:247-276.

Danforth, B.N. 1989b. Nesting behavior of four species of *Perdita* (Hymenoptera: Andrenidae). J. Kansas Entomol. Soc. 62:59-79.

Danforth, B.N. 1991a. Female foraging and intranest behavior of a communal bee, *Perdita portalis* Timberlake (Hymenoptera: Andrenidae). Ann. Entomol. Soc. Am. 84:537-548.

Danforth, B.N. 1991b. The morphology and behavior of dimorphic males in *Perdita portalis* (Hymenoptera: Andrenidae). Behav. Ecol. Sociobiol. 29:235-247.

Danforth, B.N. & J.L. Neff. 1992. Male polymorphism and polyethism in *Perdita texana* (Hymenoptera: Andrenidae). Ann. Entomol. Soc. Am. 85:616-626.

Duffield, R.M., J.W. Wheeler, & G.C. Eickwort. 1984. Sociochemicals in Bees. In: Bell, W.J. & R.T. Cardé, Chemical Ecology of Insects (pp. 387-428), Sunderland Mass.: Sinauer Associates.

Eickwort, G.C. 1969. A comparative morphological study and generic revision of the augochlorine bees (Hymenoptera: Halictidae). Univ. Kansas Sci. Bull. 48:325-524.

Farris, J.S. 1988. Hennig86, version 1.5. Distributed by the author, Port Jefferson Station, N.Y.

Fitzhugh, K. 1989. Cladistics in the fast lane. J. New York Entomol. Soc. 97:234-241.

Fox, W.J. 1893. Report on some Mexican Hymenoptera, principally from Lower California. Proc. California Acad. Sci. (Ser. 2) 4:1-25.

Harris, R.A. 1979. A glossary of surface sculpturing. Occasional Papers in Entomology, State of California Department of Food and Agriculture 28:1-31.

Heselhaus, F. 1922. Die Hautdrüsen der Apiden und verwandter Formen. Zool. Jahrb., Anat. 43:369-464

Lundberg, J.G. 1972. Wagner networks and ancestors. Syst. Zool. 21:398-413.

Maddison, W.P., M.J. Donoghue, & D.R. Maddison. 1984. Outgroup analysis and parsimony. Syst. Zool. 33:83-103.

Martin, W.C. & C.R. Hutchins. 1981. A Flora of New Mexico. v. 1. J. Cramer, Vaduz, Germany.

Mason, W.R.M. 1986. Standard drawing conventions and definitions for venation and other features of wings of Hymenoptera. Proc. Entomol. Soc. Wash. 88:1-7.

McGinley, R.J. 1986. Studies of Halictinae (Apoidea: Halictidae), I: Revision of New World *Lasioglossum* Curtis. Smithsonian Contr. Zool. 429, vi+294 pp.

Michener, C.D. 1944. Comparative external morphology, phylogeny, and classification of the bees (Hymenoptera). Bull. Amer. Mus. Natur. Hist. 82:151-326.

Michener, C.D. & A. Fraser. 1978. A comparative anatomical study of mandibular structure in bees. Univ. Kansas Sci. Bull. 51:463-482.

Nedel, J.O. 1960. Morphologie und Physiologie der Mandibeldrüse einiger Bienen-Arten (Apidae). Z. Morph. Ökol. Tiere 49:139-183.

Neff, J.L. & B.N. Danforth. 1992 (1991). The nesting and foraging behavior of *Perdita texana* Cresson (Hymenoptera: Andrenidae). J. Kansas Entomol. Soc. 64:394-405

Norden, B.B., K.V. Krombein & B.N. Danforth. 1992. Taxonomic and bionomic notes on *Perdita* (*Hexaperdita*) *graenicheri*. Journ. Hymenoptera Research 1:107-118.

Platnick, N.I. 1989. An empirical comparison of microcomputer parsimony programs, II. Cladistics 5:145-161.

Rozen, J.G., Jr. 1967. Review of the biology of panurgine bees, with observations on North American forms (Hymenoptera: Andrenidae). Amer. Mus. Novitat. no. 2297: 1-44.

Rozen, J.G., Jr. 1989. Life history studies of the "primitive" panurgine bees (Hymenoptera: Andrenidae: Panurginae). Amer. Mus. Novitat. no. 2962: 1-27.

Ruz, L. 1991. Classification and phylogenetic relationships of the panurgine bees: the Calliopsini and allies (Hymenoptera: Andrenidae). Univ. Kansas Sci. Bull. 54:209-256.

Schönitzer, K., & J. Schuberth. 1993. Occurrence and morphology of the fovea facialis and its gland in Apoidea (Hymenoptera). Mitt. Dtsch. Ges. Allg. Angew. Entomol. 8: 911-917

Schuberth, J. & J. Schönitzer. 1993. Vergleichende Morphologie der fovea facialis und der Stirnseiten druse bei Apoidea und Sphecidae (Hymenoptera: Aculeata) Linzer Biol. Beitr. 25: 205-277

Simpson, B.B. & J.L. Neff. 1987. Pollination ecology in the arid southwest. Aliso 11:417-440.

Smith, F. 1853. Catalogue of hymenopterous insects in the collection of the British Museum. Pt. 1 Andrenidae and Apidae. London: British Museum. 197 pp.

Snelling, R.R. & B.N. Danforth. 1992. A review of the *Perdita* subgenus *Macrotera* (Hymenoptera: Andrenidae). Contr. Sci., Nat. Hist. Mus. Los Angeles County 436:1-12.

Snodgrass, R.E. 1941. The male genitalia of the Hymenoptera. Smithsonian Misc. Coll. 99:1-86.

Strand, E. 1932. Miscellanea nomenclatorica zoologica et palaeontologica. IV. Folia Zoologica et Hydrobiologica 4:193-196.

Timberlake, P.H. 1953. Bees of the genus *Perdita* in the collection of the University of Kansas (Hymenoptera, Apoidea). Univ. Kansas Sci. Bull. 35:961-985.

Timberlake, P.H. 1954, 1956, 1958, 1960, 1962, 1964, 1968. A revisional study of the bees in the genus *Perdita* F. Smith with special reference to the fauna of the Pacific coast (Hymenoptera: Apoidea) I-VII. Univ. Calif. Publ. Entomol. 9:345-432, 11:247-350, 14:303-410, 17:1-156, 28:1-107, 28:125-387, 49:1-196.

Timberlake, P.H. 1971, 1980. Supplementary studies on the systematics of the genus *Perdita* (Hymenoptera, Andrenidae). I and II. Univ. Calif. Publ. Entomol. 66:1-63; 85:1-65.

Watrous, L.E. & Q.D. Wheeler. 1981. The out-group comparison method of character analysis. Syst. Zool. 30:1-11.

Wiley, E.O. 1981. Phylogenetics. John Wiley & Sons, New York.

ANNOUNCEMENT

The *University of Kansas Science Bulletin* (continuation of the *Kansas University Quarterly*) is an outlet for scholarly scientific investigations carried out at the University of Kansas or by University faculty and students. Since its inception, volumes of the *Bulletin* have been variously issued as single bound volumes, as two or three multi-paper parts or as series of individual papers. Issuance is at irregular intervals, with each volume prior to volume 50 approximately 1000 pages in length. Effective with volume 50, page size has been enlarged, reducing the length of each volume to about 750 pages.

The supply of all volumes of the *Kansas University Quarterly* is now exhausted. However, most volumes of the *University of Kansas Science Bulletin* are still available and are offered, in exchange for similar publications, to learned societies, colleges and universities and other institutions, or may be purchased at $30.00 per volume. Where some of these volumes were issued in parts, individual parts are priced at the rate of 3 cents per page. Current policy, initiated with volume 46, is to issue individual papers as published. Such separata may be purchased individually at the rate of 7 cents per page, with a minimum charge of $1.50 per separate. Subscriptions for forthcoming volumes may be entered at the rate of $30.00 per volume. All communications regarding exchanges, sales and subscriptions should be addressed to the EXCHANGE LIBRARIAN, UNIVERSITY OF KANSAS LIBRARIES, LAWRENCE, KANSAS 66045.

Reprints of individual papers for personal use by investigators are available for most recent and many older issues of the *Bulletin*. Such requests should be directed to the author.

The International Standard Serial Number of this publication is US ISSN 0022-8850.

Editor
Charles D. Michener

Editorial Board
Meredith Lane, *Chairman*
James S. Ashe
George W. Byers
Christopher Haufler
Norman A. Slade

This issue, vol. 55, no. 16, is the last to be published under the title "University of Kansas Science Bulletin."

The publication program will be continued as part of a new series entitled "Scientific Papers, University of Kansas Natural History Museum." Exchanges and subscriptions will be continued through the University of Kansas Library.

3 2044 093 362 382